

An Investigation into the Decline of the Bearded Vulture

***Gypaetus barbatus* in Southern Africa**



Sonja C. Krüger

August 2014

Dissertation presented for the degree of Doctor of Philosophy
Percy FitzPatrick Institute of African Ornithology
DST/NRF Centre of Excellence
Department of Biological Sciences, Faculty of Science
University of Cape Town

Supervised by Dr. Arjun Amar and Dr. Robert E. Simmons



The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

Recommended citation:

Krüger SC (2014) An Investigation into the Decline of the Bearded Vulture *Gypaetus barbatus* in Southern Africa. PhD Thesis, Percy FitzPatrick Institute, University of Cape Town, South Africa, pp 235.

Declaration

This dissertation reports original research that I conducted under the auspices of the Percy FitzPatrick Institute, University of Cape Town. I declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own both in conception and execution. The work was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and with the approval of the Animal Ethics Committee. This work has not been submitted in any form for a degree at another university.

Signed by candidate

Signature Removed

.....
Signed: Sonja C. Krüger

15/08/2014

.....
Date:

Table of Contents

Abstract.....	viii
Acknowledgements.....	x
Chapter 1: Introduction.....	1
Chapter 2: Trends in territory occupancy, distribution and density of the Bearded Vulture <i>Gypaetus barbatus</i> in southern Africa.....	35
Abstract	37
Introduction.....	37
Methods.....	41
Census of Former and Current Breeding Territories	41
Estimating Territory Occupancy and Population Size.....	43
Estimating Breeding Distribution and Density.....	45
Estimating Encounter Rates	45
Core versus Peripheral Territories.....	45
Statistical Analyses	46
Results	46
Territory Occupancy and Population Size	46
Current Population Estimate	50
Breeding Distribution and Density	50
Core versus Peripheral Territories.....	53
Discussion	55
Acknowledgements	58
References	59
Appendices.....	66
Chapter 3: Anthropogenic activities influence the abandonment of Bearded Vulture <i>Gypaetus barbatus</i> territories in southern Africa.....	69
Abstract	71
Introduction.....	71
Methods.....	75
Study Area	75
Extraction of Covariates Surrounding Each Territory	76
Statistical Analyses	79
Results	80
Influence of Environmental Variables on Territorial Abandonment.....	81
Discussion	88
Acknowledgements	92

References	92
Appendices.....	101
Chapter 4: Differential range use and anthropogenic risk exposure between age classes of southern African Bearded Vultures <i>Gypaetus barbatus</i>	105
Abstract	107
Introduction.....	107
Methods.....	111
Capture and Marking	111
Ethics Statement.....	114
Spatial and Temporal Analyses	114
Home Range Size.....	115
Home Range Use	116
Estimating Exposure to Risks and Benefits between Age Classes	116
Results	119
Home Range Size.....	119
Home Range Use	125
Comparison of Exposure to Risks and Benefits between Age Classes.....	127
Discussion	128
Acknowledgements	133
References	134
Appendices.....	144
Chapter 5: Genetic structure in the Bearded Vulture <i>Gypaetus barbatus</i> : reduced diversity in southern Africa	147
Abstract	149
Introduction.....	149
Methods.....	151
Samples.....	151
DNA Isolation, Polymerase Chain Reaction (PCR) and Sequencing	151
Analyses	151
Results	152
Discussion	153
Acknowledgements	157
References	157
Appendices.....	161
Chapter 6: Poisoning increases the extinction risk of the Bearded Vulture <i>Gypaetus barbatus</i> in southern Africa	163

Abstract	165
Introduction.....	166
Methods.....	168
Age Structure	170
Productivity	171
Estimation of Survival Rates.....	173
Quantifying Causes of Mortality	174
Population Modelling	175
Statistical Analyses.....	176
Results	176
Age Structure.....	176
Productivity	177
Annual Survival Estimates and Causes of Mortality	179
Population Growth Rate.....	181
Discussion	186
Acknowledgements	191
References	192
Appendices.....	201
Chapter 7: Discussion	203
Conclusions.....	216

Abstract

The Bearded Vulture *Gypaetus barbatus* is a Critically Endangered species in southern Africa whose entire range in the Southern Hemisphere falls within the Maloti-Drakensberg mountains of South Africa and Lesotho, which forms the area of focus for this research. In this thesis I have attempted to synthesize 15 years of research on the Bearded Vulture population of southern Africa using various approaches to quantify the decline in the species, investigate the mechanisms of this decline and determine the most appropriate management actions necessary to attain the short-term species' conservation target of a positive population growth rate.

Firstly I assessed the territory occupancy, distribution and density of the population over two time periods to identify population trends. The number of occupied territories decreased by between 32%-51%, the breeding range decreased by 27% and breeding densities decreased by 20% over the past five decades. The birds occupy a breeding range of 28,125 km² with higher densities recorded in the core of the range than in the peripheral areas. The population is estimated at between 368-408 individuals (109-221 breeding pairs).

Three hypotheses were then examined in an attempt to explain which factors were associated with territories recorded as abandoned; those related to human impact, food availability and climate change. Of the seven covariates examined within the home range of an adult pair using a model selection process using Akaike's Information Criterion, the strongest support was for the human impact hypothesis, with abandonment more likely in territories with higher densities of power lines and human settlements. These findings were in accordance with the main causes of mortality.

The movements of all age classes were investigated using data from satellite transmitters affixed to 18 birds to determine exposure to perceived benefits or anthropogenic risks. The overall foraging range of the population was estimated to be 51,767 km² and non-adults were found to use 65% of this area whereas adults focussed their activities in an area

of about 286 km² around their nests. Non-adults increased the size of their range as they aged, with birds aged between 4-6 years facing the greatest exposure to risk factors.

The genetic risk was examined by sampling two populations in sub-Saharan Africa to ascertain genetic variation, evolutionary placement and connectivity using Mitochondrial DNA fragment analyses. My results showed little to no differentiation between populations in southern Africa and Ethiopia suggesting that translocations of individuals from Ethiopia could be considered for introduction into the local population. The reduced haplotype diversity found in southern Africa suggests that translocations may be necessary to improve genetic diversity.

Lastly I used population viability analysis models to determine the future population trend and identify the primary demographic and environmental constraints on the population. The models predicted a negative growth rate for the population over the next 50 years ($\lambda=0.99$) with a high probability (0.89) of extinction as a result of low survival estimates (particularly for adults; 86%) and reduced productivity (55%). Human activities (69%) and power line collisions (21%) were the primary reasons for the low survival rates with poisoning alone accounting for 90% of the deaths. To achieve a positive growth rate, mortality rates should be reduced by >50%, productivity increased by >25% and the population should be supplemented by at least six individuals annually for the next 20 years.

Several recommendations are listed to address the primary threat of poisoning and continued monitoring of the population is essential to evaluate the success of the implementation of these recommendations. My research demonstrates the importance of focussing on small populations, declining populations and populations at the periphery of the species' range and my results confirm that urgent intervention is required to improve the status of the population. My findings also contribute to achieving vulture conservation objectives regionally, continentally and internationally.

Acknowledgements

My involvement with Bearded Vultures began in 2000 following discussions with Peter Chadwick, Peter Openshaw and Douglas van Zyl from Ezemvelo KwaZulu-Natal Wildlife around the status of the species that was iconic to the Drakensberg Park. These discussions grew into what eventually became the Maloti Drakensberg Vulture Project, a project which has involved and inspired many individuals since its inception. It is impossible to thank all those who have been involved between 2000-2014, but everyone's contributions along the way are hugely appreciated.

Steven Piper and Colleen Downs encouraged me to embark on the PhD journey and Rob Simmons was instrumental in registering me with the Percy FitzPatrick Institute. Arjun Amar took me on as his first student upon arriving in the country. I have benefitted enormously from having Arjun as a supervisor and have enjoyed the experience of being a student again. Thank you for the many hours of discussion, advice and assistance.

I am grateful to my parents for providing me with the opportunities in life that have led to achieving this goal. They have supported and encouraged me along the way and also accompanied me on many field trips and assisted with many related errands. My brother and nieces also provided company during monitoring trips and vulture capture quests.

My employers, Ezemvelo KwaZulu-Natal Wildlife, and my supervisor Ian Rushworth are thanked for recognizing the importance of this research and generously providing resources to support my work throughout. I am also grateful to the Wildlands Conservation Trust, the Maloti Drakensberg Transfrontier Programme, Sasol through the Endangered Wildlife Trust and the South African National Park's staff of Golden Gate Highlands National Park for the funding and support received for the Maloti Drakensberg Vulture Project over the years. André Botha from the Birds of Prey Working Group of the Endangered Wildlife Trust and the Bearded Vulture Task Force members are thanked for their hard work since 2006 towards achieving the objectives of the species' management plan. Mpiti Letsie,

Makhubu Shobana and Samuel Zwakala have undertaken valuable monitoring and advocacy work in Lesotho over the years. Joyce Loza was extremely helpful in the process of getting the Biodiversity Management Plan for the Species approved.

I am grateful for the tireless efforts of many individuals during endless hours spent trying to capture birds. Alfonso Godino, Allan Howell and Daniel Hegglin were involved in the initial stages (2007 and 2008) and were instrumental in perfecting the capture technique and teaching me to make and fit harnesses. Carmen Callero flew out from Spain several years in a row to share long, cold hours in a hide or in the 'Yeti suit'. Ben Hoffman and Rickert van der Westhuizen assisted with captures for weeks on end and Rickert assisted with data collation and dissemination for many years post capture. Thank you to Charl Brummer, David Allan and Tim O'Connor who spent precarious moments dangling on ropes while grappling with chicks or equipment in the nest. Many Ezemvelo KwaZulu-Natal Wildlife staff of the Maloti Drakensberg Park World Heritage Site spent countless hours hiking to nests with me in mid-winter or monitoring the sites in their respective sections. John Crowson is thanked for his kidney jarring trips to monitor nesting success at sites in Lesotho best seen from the air!

My thanks to Shannon Hoffman for being the custodian of 'our' captive bird and playing such an important advocacy role. Hans Frey and Alex Llopis were also always available to answer questions on Bearded Vultures in captivity. I enjoyed my trips to the University of Johannesburg to work on the genetic aspect of the project- thanks to Bettine Jansen van Vuuren for teaching me DNA extraction! I also appreciate the efforts of Phillip Lennon from Coral Tree Films in telling the story of the Bearded Vulture following his many trips to film our work in the field.

One of the highlights of registering to undertake my PhD through University of Cape Town were the frequent trips to Cape Town and the opportunity to visit my good friends from Pietermaritzburg University days who were always willing to host and make me feel welcome. Thank you Shane Murray, Jean Tukker and Shan Silberbauer for sharing your

families and homes with me over the years. Thanks also to my friends back home for their patience over the years while I was working instead of socializing, especially to Shane Elliott who was always keen to accompany me when searching for a downed transmitter or when monitoring trips promised great photo opportunities or 4x4 challenges. Many of the photos in this thesis are the results of some memorable trips. I have him to 'thank' for getting me into trail running which provided a pleasant break from the books in the final year of write-up.

Lastly the birds themselves that were very challenging to catch between 2007 and 2013 and have provided the most incredible data since: Daniel (the first bird caught after six weeks of patient waiting) chewed off his transmitter after 10 months; Barbara's fate remains unknown after her transmitter stopped working 30 days later; Andalucia was killed and the transmitter buried; the chicks Linong and Ikloba from Lesotho both found poisoned in the same area in the Eastern Cape about a year apart; Connor's fate is unknown after the transmitter stopped within 10 days of fitting it in the nest; Wandervogel the last remaining chick still flying after five years; Lehlwa (caught in the snow) and Inkozi caught as juveniles five years ago- the longest lasting birds and transmitters so far!; Olivia died of poisoning in Lesotho; Zakhumi (caught during the 2010 Soccer World Cup) and Aspen died of poisoning in Free State; Bardbek was found poisoned after only one month; Blue-boy (Umcociathafa) whose extensive movements fascinated all until he flew into a power line; adults Sphinx and Lefuma both found poisoned a few kilometres from their nests in KwaZulu-Natal and Free State respectively; adult Carmella chewed her transmitter off after two years; adults Pharoah, Jeremia and Springbok (caught as a sub-adult and bred a year later) still flying; and juveniles Mac, Mollie, Camo and Kloutjie (whose claw went through my finger) the last juveniles to be caught and which are still at large. Finally our captive bird Leseli, confiscated from a roadside chicken-coop, fulfilling her role admirably as the species' ambassador.

Although these birds carry a 100 g burden, the cost to the individual is far outweighed by the benefits obtained from the tracking devices for the conservation of the population as a whole. My hope is that talks given to interest groups in future will be a lot less depressing!

Chapter 1: Introduction



Photo 1 Juvenile Bearded Vulture landing on a Drakensberg cliff

The world's biota are in catastrophic decline because anthropogenic activities are continually altering the essential habitats and ecosystems on which species depend (Butchart *et al.* 2010, Hoffman *et al.* 2010). One-fifth of the world's vertebrates are threatened with extinction (Hoffman *et al.* 2010) and one in eight of the world's bird species is deemed globally threatened (BirdLife International 2013). Land use change, the most common cause of habitat degradation, is expanding, and overharvesting, pollution, urbanisation and climate change are increasing the rate of species loss (Sutherland *et al.* 2011) such that extinction rates are exceeding the normal background rates by a few orders of magnitude (Pimm *et al.* 1995). These threats are intensifying as technology continues to improve and the human population continues to increase (UN Environment Programme 2007). This wave of anthropogenically driven biodiversity loss, aptly termed the "Anthropocene defaunation" by Dirzo *et al.* (2014), has major consequences for the ecosystem functions and services on which we depend as well as having evolutionary consequences (Naeem and Wright 2003, Dirzo *et al.* 2014, Seddon *et al.* 2014, Vignieri 2014).

Global Scavenger declines

The scavenger guild is threatened around the globe (Hoffmann *et al.* 2010). Numerous studies have shown that mammalian scavengers are facing persecution as a result of human-wildlife conflict (Newmark *et al.* 1994, Woodroffe 2000, Kissui 2008, Watts and Holekamp 2009). For example, hyaena are being poisoned by African pastoralists for killing their livestock (Woodroffe 2000) and human persecution is the greatest threat to the persistence of these scavengers (Woodroffe and Ginsberg 1998). Avian scavengers too are facing human persecution and have the highest percentage of extinction-prone species among avian functional groups (Sekercioglu *et al.* 2004). Vulture populations in particular are one of the fastest declining groups of birds (Green *et al.* 2004, Oaks *et al.* 2004, Ogada 2014).

Both new world (Cathartidae) and old world (Accipitridae) vultures have experienced large population declines worldwide from a variety of human related factors which have resulted in the loss of suitable breeding and foraging habitat and poisoning (Mingozzi and Estève 1997, Herremans and Herremans-Tonnoyer 2000, Green *et al.* 2004, Thiollay 2006, Ogada *et al.* 2012). For example, the California Condor *Gymnogyps californianus* was virtually extirpated in the wild (Ogden 1985) and the Oriental White-backed Vulture *Gyps bengalensis* declined by >95% over two decades from the 1990s followed by declines of other *Gyps* species in Asia (Green *et al.* 2004, Oaks *et al.* 2004), resulting in these species being listed as Critically Endangered (BirdLife International 2001). The Asian vulture declines were attributed to the toxic effects of the veterinary drug diclofenac, a non-steroidal anti-inflammatory drug, from feeding on ungulates treated with the drug shortly before death (Green *et al.* 2004). Once the cause of the decline had been established the conservation measures that were successfully implemented included banning veterinary diclofenac in 2006 and promoting an alternative non-lethal veterinary drug (meloxicam), establishing captive populations of all three affected *Gyps* species and supplementary feeding (Pain *et al.* 2008). The success of these conservation measures was evident a few years later in the increased productivity of several populations of Indian vultures *G. indicus* (Jamshed *et al.* 2012).

Biodiversity loss is widely recognized as hindering ecosystem functioning worldwide (Naeem and Wright 2003, Dirzo *et al.* 2014) and scavengers provide an important suite of ecosystem services and key ecological functions such as waste removal, disease control and nutrient recycling (Houston and Cooper 1975, DeVault *et al.* 2003). The loss of obligate scavengers, such as vultures, can therefore have major ecological, social and economic consequences. Ecologically the absence of vultures may affect the community composition of scavengers at carcasses which could alter scavenging rates for individual species (Ogada *et al.* 2012), and result in an increase of opportunistic species at carcasses such as feral dogs (Pain *et al.* 2003). Socially, vultures are significant amongst the Parsi community where they dispose of human corpses left in the open to be scavenged (Markandya *et al.* 2008).

Economically, the increased potential for disease transmission at carcasses will result in increased costs to human health (Ogada *et al.* 2011).

The Asian Vulture Crisis and the consequences of the loss of these obligate scavengers has generated considerable concern and subsequent interest in vulture research in recent years, particularly in Africa (Koenig 2006, Ogada *et al.* 2011).

African Vulture Crisis

Recent research has shown that Africa too is experiencing the silent but rapid demise of its vultures (Virani *et al.* 2011, Ogada *et al.* 2012), a wildlife crisis that is little-known, poorly understood, and often-ignored. Vultures were once common and widespread across the continent, but over the past 30 years declines of up to 97% have been detected for some species in West Africa while declines of 50-60% have been recorded in the East and southern African savannahs (Ogada *et al.* 2012). Africa is home to 11 of the 23 species of vultures worldwide of which four species (36%) are currently listed as globally Endangered and at risk of extinction, and three are listed as Vulnerable (BirdLife International 2014). The indiscriminate use of poison is one of the major causes of the recent declines in vulture populations across most of Africa (Virani *et al.* 2011, Roxburgh and McDougall 2012, Ogada 2014), although the rates of decline and causes of poisoning differ across the continent. In East and southern Africa vultures die after eating carcasses that have been intentionally poisoned to control feral dog populations and carnivores such as jackals and hyaenas (Virani *et al.* 2011, Ogada *et al.* 2012). Vultures are targeted directly (through poisoning or other means) for food (Thiollay 2006), for the traditional medicine trade (Mander *et al.* 2007) or to prevent law enforcement agents being attracted to carcasses through the conspicuous presence of vultures (Lipiya 2011, Roxburgh and McDougall 2012).

Vultures are protected species in most African countries but enforcement of the legislation is poor. In order to address the potential “African Vulture Crisis”, the Vulture Specialist Group of the IUCN Species Survival Commission was established in 2011 to

ensure the continued survival of vultures across the African continent. The Group aims to assess the population status of all African vulture species, identify threats and implement appropriate conservation actions that effectively address the key threats to African vultures. Immediate action is essential because “without rapid and effective action, Africa will soon lose these critical keystone species!” (J. Tavares *pers. comm.*, Director of the Vulture Conservation Foundation).

Given the consequences of these ongoing and severe declines of vulture populations globally and in Africa, decisions on how to manage threatened species are central to reducing the extinction risk and loss of biodiversity. Scientific information on threatened species is essential to inform conservation management decisions and develop and implement effective policies and actions to address the declines (Fleishman *et al.* 2011). To maximize the value of scientific research to decision makers, the most pertinent research questions must be addressed and recommendations for remedial action must be prioritised to ensure the best use of limited resources for the management of threatened species (Fleishman *et al.* 2011).

Single-Species Conservation

In recent years conservation research and management have often moved away from focussing on single species toward entire ecosystems or ecological processes. The main reason for this paradigm shift was the need for conservation to become more economically efficient in an era of increasing conservation needs and decreasing budgets. A strategy focussing on ecosystem/process management aimed to achieve this, with the notion that it would effectively address all possible issues of species and habitat conservation (Meffe and Carroll 1994, Simberloff 1997). However, there are some fundamental flaws in this approach. For example, Tracy and Brussard (1994) showed that many ecosystem processes can be preserved even though the component species normally responsible for them are

lost, which means that preventing species' extinctions does not hold the same significance. Thus, I would argue that there is still very much a place for single-species conservation undertaken in tandem with the conservation of ecosystems and ecological processes. Furthermore, single-species studies still provide invaluable information for that species, even if they do not represent the ecological and conservation needs of other species (e.g. Andelman and Fagan 2000, Lindenmayer *et al.* 2002, Roberge and Angelstam 2004, Branton and Richardson 2010, Isasi-Catala 2011). Many questions can only be addressed at the species level which may be useful if these species are 'umbrella' species. Umbrella species are typically large, require a lot of habitat and generally share many living requirements with other organisms in their range so that by protecting a larger area, other species are protected as well (Shrader-Frechette and McCoy 1993).

Moreover, legislation is also often still species focussed and many species will require specific and targeted interventions to persist in the face of the current threats of habitat loss and climate change (McLachlan *et al.* 2007). The fact that many species-specific long-term monitoring programmes are in place, makes it currently possible to monitor species' range shifts in relation to climate change (Thomas *et al.* 2004, Parmesan and Yohe 2003). Therefore if we want to maintain all the biological components of an intact ecosystem, we need to undertake autecological research, focussed on the individual species and its environment. When it comes to the management of threatened species, an understanding of the causes of decline are essential to reduce the risk of extinction and further loss of biodiversity (Norris 2004).

Small and Declining Populations

Effective species management requires an understanding of how a population has declined and what the past, present and future causes of decline are in order to implement management strategies to address the decline. This understanding is the basis of Caughley's (1994) declining-population paradigm. Caughley (1994) also identified the small-

population paradigm that attempts to understand the influence of population size on population persistence. Both paradigms are important in saving threatened species from extinction (Hedrick *et al.* 1996) and should not be considered in isolation. For example, studies on inbreeding effects have shown the importance of the small-population paradigm in understanding the population biology of wild populations (Madsen *et al.* 1999) and population restoration (Keller and Waller 2002), and Green (1995, 2002) and Balmford (1996) have shown the importance of the declining population paradigm in understanding the anthropogenic effects on wild populations and designing management strategies for these.

A population's decline can be categorised into three phases within which conservationists can intervene (Norris 2004). In Phase 1, conservationists quantify the likelihood of a population declining in the future based on environmental conditions; in Phase 2 conservationists work with populations in the process of declining; and in Phase 3 conservationists work with populations that have stabilized at low abundance levels following a decline. In phases 2 and 3 the conservation aims are to halt the decline and increase abundance respectively, to improve population persistence. For most populations that continue to decline to critically low levels of abundance, the urgency for action and a lack of data often preclude a detailed analysis of the causes of decline (Norris 2004). In these cases, maintaining the population through the bottleneck becomes the primary aim of management in the short term but in the longer term the putative causes of the decline may need to be established in order to restore populations in the wild. To assess how management strategies might assist conservationists, Norris (2004) advocates the use of ecological tools such as statistical models of habitat use, demographic models and behaviour-based models which assess the causes of decline and then examine the effectiveness of various strategies to address this decline.

In my thesis I detail research undertaken on the declining Bearded Vulture *Gypaetus barbatus* population at the southern tip of Africa and try to unify the small and declining population paradigms by using ecological tools to assess the causes of decline and identify

remedial action, as well as determining the genetic diversity and placement of the population to add further value to conservation management strategies.

Study Species: The Bearded Vulture

The Bearded Vulture *Gypaetus barbatus* (Linnaeus 1758) (Figure 1.1) is a large accipitrid raptor that inhabits mainly mountainous regions of Eurasia and Africa (Cramp and Simmons 1980) (Figure 1.2). It is a non-colonial, monogamous, sexually monomorphic cliff-nester and pairs occupy a territory containing one or more nests on high cliffs generally above 1,800 m above sea level (Heredia 1991, Bustamante 1996, Brown 1997, García *et al.* 2009). The species occupies a unique avian trophic guild in that it is a scavenger whose diet consists almost exclusively of bones from the carcasses of wild and domestic ungulates (Hiraldo *et al.* 1979, Margalida *et al.* 2007). They forage along ridges and valleys in protected areas but also over communal rangelands and commercial farming areas.



Figure 1.1 A juvenile (left) and an adult (right) Bearded Vulture *Gypaetus barbatus* (Linnaeus 1758).

Two sub-species are recognised based on plumage characteristics (Hiraldo *et al.* 1984, Mundy *et al.* 1992). *G. b. barbatus* occurs north of the Tropic of Cancer while *G. b. meridionalis* occurs south of the Tropic of Cancer. In sub-Saharan Africa the species occurs in small geographically isolated populations in South Africa and Lesotho, East Africa and Ethiopia.



Figure 1.2 Global distribution of the Bearded Vulture *Gypaetus barbatus* (source:www.planetofbirds.com).

Globally the species has been uplisted from Least Concern to Near Threatened (BirdLife International 2014) because although it is recovering in Europe, it is declining globally as a result of poisoning, disturbance and collisions with power lines. The global population estimate is 1,300-6,700 mature individuals (BirdLife International 2014) of which <1,300 are estimated to occur in sub-Saharan Africa. Poisoning, both direct and indirect as well as habitat degradation, disturbance at breeding sites and collisions with power lines are considered to be the main global threats (Ferguson-Lees and Christie 2001).

In southern Africa, there was a drastic decline in both the population number and the range between 1700-1969 (Boshoff *et al.* 1978, Brooke 1984) resulting in the contraction of the species' range from the south-western Cape to a more restricted area in the highlands of Lesotho and immediately adjacent Maloti-Drakensberg mountains (Brown 1990) (Figure 1.3). The reasons given for the large range contraction were persecution and displacement by humans and livestock at lower altitudes and the degradation of many of its habitats which resulted in the species being classed as "rare and threatened" by Siegfried *et al.* (1976). Population numbers continued to decline during 1970-2000 resulting in the species being uplisted to Endangered (Anderson 2000) with the main cause of mortality attributed to poisoning (Brown 1991). This re-classification was attributed to the Bearded Vultures' small and declining population size, restricted range, range contraction, and the susceptibility to several threats (e.g. persecution, poisoning, collisions with power lines) in Lesotho and South Africa.

Study Area 'Maloti-Drakensberg Mountain Region of Southern Africa' and Methods

The Maloti-Drakensberg region of southern Africa spans the highlands and the Maloti Mountains of Lesotho and the Drakensberg mountain range in South Africa which extends from the north-eastern Free State province in the north, through the eastern boundary of KwaZulu-Natal with Lesotho in the east, to the northern part of the Eastern Cape province in the south (Figure 1.3).

There is great variation in the topography of the Maloti-Drakensberg mountains with summit plateaux and peaks, vast basalt and sandstone cliffs, deep valleys and intervening spurs with an average altitude of 2,200 m (1,280 m–3,500 m) (Sycholt 2002). The range in topography has resulted in the establishment of diverse vegetation communities within which are habitats with a remarkable richness of plant and animal species, many of which are endemic and internationally recognised threatened species, such as the Bearded Vulture.

A large portion of the international boundary between KwaZulu-Natal and Lesotho

forms the eastern boundary of the Maloti Drakensberg Park, an inland mountain protected area totalling 242,813 ha which received World Heritage Status in 1999 for both its natural and cultural values (Figure 1.3).

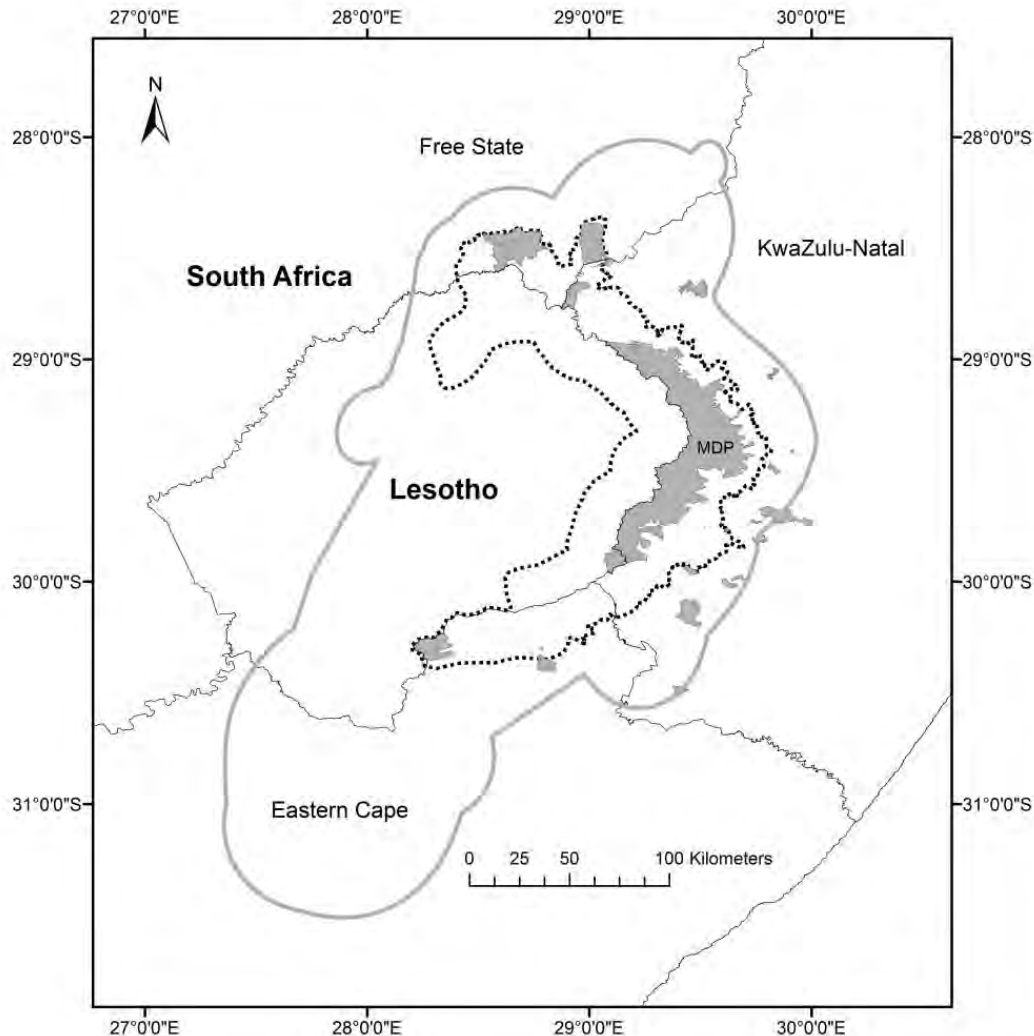


Figure 1.3 The Bearded Vulture's distribution range (-) in southern Africa, between 27°00"–30°00" E and 28°00"–31°40" S. Protected areas are shaded in grey with the Maloti Drakensberg Park (MDP) being the largest protected area along the KwaZulu-Natal/Lesotho border within the Maloti Drakensberg Transfrontier Programme Area (...).

The park is owned by the state and managed by the provincial conservation body, Ezemvelo KwaZulu-Natal Wildlife. The park also forms part of a Transfrontier Park with Sehlabathebe National Park in Lesotho, and falls within the Maloti Drakensberg Transfrontier Programme

area. The purpose of the park is to contribute to the achievement of provincial and national conservation targets through protecting endangered, rare and endemic species indigenous to the area. One such species is the Bearded Vulture which nests along the escarpment throughout the park. In order to develop conservation targets for this endangered species, information on the current status of the population in the park was required. For this reason a monitoring programme was implemented by Ezemvelo KwaZulu-Natal Wildlife in 2000 to assess the population status of the Bearded Vulture, both within the Maloti Drakensberg Park and also in the wider province of KwaZulu-Natal. Initial monitoring results (2000-2005) indicated a continued decline in the population (Krüger 2006) which raised concern amongst the conservation authorities. Similar declines were also recorded in Lesotho (Allan and Jenkins 2005). Apart from the Endangered status of the species, it is also an emblematic species, forming part the Maloti Drakensberg Park logo (Figure 1.4) and is an icon for the Maloti Drakensberg Transfrontier Programme because it epitomises cross-boundary collaboration and initiatives. For these reasons, Ezemvelo KwaZulu-Natal Wildlife, the implementing agent of the Transfrontier Programme, identified the need for further action to address the suspected continued decline in the species. As a result the Maloti Drakensberg Vulture Project was established aimed at conserving the Bearded and Cape Vulture *Gyps coprotheres* in the Maloti-Drakensberg region.



Figure 1.4 The Bearded Vulture forms the focal point of the Maloti Drakensberg Park's logo.

Land use in the study area, beyond the protected area boundaries, comprises predominantly livestock grazing on communal grazing lands in Lesotho or commercial livestock farms and communal lands in South Africa. Wild ungulates are at low densities on communal and commercial lands and are scavenged predominantly from protected areas, although densities in these areas are naturally low.

Background to Bearded Vulture Conservation in Southern Africa

Detailed research was undertaken on the species by Christopher Brown during 1980-1983 which included the first in-depth study of the biology of the species in southern Africa (Brown 1988, Brown 1990), its distribution and status (Brown 1992), the demography (Brown 1997) and the reasons for decline (Brown 1991). During his study period C. Brown was based in the central portion of the Maloti Drakensberg Park where most of his research was undertaken, with the occasional trip to other parts of the species' range. Estimates of breeding pairs, breeding density, demographic parameters and home-range were based on his observations in the primary study area and from radio-tracked birds caught in this area. Distribution and density estimates also included information from questionnaire surveys conducted throughout the range. During his study period, efforts were made to educate landowners/managers on the status of, and threats to, the species, with the aim of reducing the threat of persecution. However, despite these efforts, it is clear from monitoring during 2000-2005 (Allan and Jenkins 2005, Krüger 2006) that there has been limited success in addressing the species' decline since the early 1980s and that the recommendations of Brown (1991) have been largely ignored. Although several individuals undertook nest site surveys (see Appendix 2.1, Chapter 2) or conducted desktop modelling exercises (Whitley 1998), no detailed research was undertaken on the species until the early 2000s when the Maloti Drakensberg Vulture Project was established.

To address the lack of conservation action, a workshop was held in 2006 facilitated by the Conservation Breeding Specialist Group who used a Population and Habitat Viability Assessment process to undertake a risk assessment and develop a species' management strategy. The goals of the workshop were to i) set a conservation target for the southern African population of Bearded Vulture and ii) determine the priority conservation interventions required to achieve the target over a ten year period. To this end the key issues facing the survival of the Bearded Vulture were identified and a list of prioritised solutions and goals were developed including detailed action plans and steps that would contribute to achieving these goals. The workshop results were detailed in a management strategy for the species from 2006-2011 (Krüger *et al.* 2006). To ensure that the action plans were implemented, the Bearded Vulture Task Force was established by the Birds of Prey Programme of the Endangered Wildlife Trust. The task force comprises representatives from conservation institutions and the scientific community as well as a number of volunteers from both Lesotho and South Africa.

In 2011 the management strategy for the species was revised and a Biodiversity Management Plan for the Species (BMP-S) (Krüger 2013) was prepared in its place to provide a more formal mechanism to achieve the species' conservation objectives. The plan was developed using regulations of the National Environmental Management: Biodiversity Act No. 10 of 2004 for Threatened or Protected Species developed by the national Department of Environmental Affairs and Tourism of South Africa who recognised the need for conservation action and developed the requisite legal framework catering for the protection of important species. The BMP-S is a mandate obtained through an approval process which provides a coordinated framework to ensure commitment from all role players in implementing the actions required to benefit the species and its habitat. The development of the BMP-S was an open and inclusive process including decision makers and researchers who reported on progress on actions from the previous plan and developed further actions required to achieve the species' targets. Although the BMP-S follows the structure provided

for within the South African legal framework, the aims, objectives and operational goals were developed for the entire population which ranges across both South Africa and Lesotho. The aim of the BMP-S is to provide a mechanism to ensure the long term survival of the species through halting the population decline and stabilizing the population at the current population size (approximately 100 breeding pairs) over the next ten years and to start growing the population to a realistic carrying capacity (150 breeding pairs) in the future.

This thesis details the research that has contributed directly to helping achieve the goals of the 2006-2011 and the 2011-2016 management frameworks as well as the aims of the Endangered Wildlife Trust's Birds of Prey Programme and the IUCN's Vulture Specialist Group.

Current Conservation Context for the Species

The Bearded Vulture has a wide global distribution of which the southern African population is at the periphery of the global range, and is the only functioning population in the Southern Hemisphere. Together with its global status of Near Threatened (BirdLife International 2014), this begs the question whether the small, declining and peripheral southern African population warrants targeted research and conservation efforts.

The justification for the conservation of this population is three fold. Firstly the species is regionally threatened and classified as Endangered (Anderson 2000) and the entire population of southern Africa occurs within the study area. Secondly, two subspecies (Mundy *et al.* 1992) and two lineages (Godoy *et al.* 2004) are recognised, therefore there is additional merit in conserving the lineages represented in sub-Saharan Africa. Thirdly, there is value in conserving peripheral populations. Populations at the periphery of the geographic range of a species have generally been regarded as having little value in conserving biodiversity because they are more vulnerable to extinction and have lower genetic diversity than those in the core of the range (Channell 2004). Recent research, however, suggests

that peripheral populations may play an important role in conserving declining species (Lomolino and Channell 1995, Lomolino and Perault 1998). Contrary to expectations, in species that have undergone large range contractions, peripheral populations persist significantly more often than do the central populations and genetic diversity may not necessarily be lower which suggests that the distinction between central and peripheral populations may not be an important distinction for conserving biodiversity and that conservation plans should include peripheral populations (Channell 2004).

A number of authorities are mandated with biodiversity conservation within the Bearded Vulture's range. In Lesotho, the Ministry of Environment Tourism and Culture is responsible for biodiversity conservation within the 10 districts that are part of the Bearded Vulture's range in that country. In South Africa, both national (Department of Environmental Affairs and Tourism) and provincial authorities are responsible for biodiversity conservation in the three provinces; Free State (South African National Parks; Free State Economic Development, Tourism and Environmental Affairs), KwaZulu-Natal (Ezemvelo KwaZulu-Natal Wildlife) and Eastern Cape (Eastern Cape Parks Board; Department of Economic Development, Environmental Affairs and Tourism). Although there are differences in the national and provincial legislation between the countries and provinces, the species is specially protected at a national level in both countries. The conservation challenge, however, is enforcing the legislation throughout the range and coordinating conservation efforts between the various authorities within the realm of budget and manpower constraints. Although the species has an important ecological role and is a transfrontier icon, the reality of resource limitations makes the transition from management planning to conservation action particularly challenging.

The Kingdom of Lesotho is a constitutional monarchy that is geographically entirely surrounded by South Africa. Economic growth is slow with many developmental challenges, institutional capacity is weak and poverty and inequality are recurring challenges with *ca.* 43% of the population living below US\$1.25 per person per day (African Development Bank

Group 2013). High food insecurity levels together with a high HIV prevalence have contributed to deteriorating social indicators, especially life expectancy. Although the Bearded Vulture is a specially protected species in Lesotho, the conservation thereof is competing with basic human welfare concerns. South Africa on the other hand is experiencing steady economic growth with only 14% of the population living below US\$1.25 per person per day even though levels of unemployment, poverty and inequality are also high. Access to basic social services is relatively high and the country has a much better institutional capacity than its neighbour (African Development Bank Group 2012). The conservation challenge in South Africa is one of gaining support for a species that is not geographically widespread or well-known, amidst a country-wide rhino poaching crisis which is at the forefront of political, public and conservation agendas. These challenges highlight the importance of this research in identifying the mechanisms of the decline of the Endangered Bearded Vulture and using the results to recommend actions aimed at raising the profile of the species and using limited resources in the most effective manner.

The Asian Vulture Crisis provides a good example of where scientific research was core to the protection and boosting of the remaining vulture populations through identifying the cause of the decline and disseminating information to government authorities to canvas the necessary financial and legislative support (Ogada *et al.* 2012). The Asian example is, however, also an indication of how in the absence of widespread bird population monitoring, it proved difficult to measure the declines and identify when and where they began.

Bearded Vulture conservation efforts in Europe over the past 30+ years also provide good examples of adaptive management where conservation actions, coupled with intensive research and monitoring, have been successful in re-establishing populations or increasing numbers in existing populations (e.g. Heredia and Heredia 1999, Hirzel *et al.* 2004, Donazar *et al.* 2009, Schaub *et al.* 2009, Cortez-Avazida *et al.* 2010).

Thesis Overview

My thesis aims to understand the limits to population growth, the reproductive success and the movements of the Bearded Vulture in southern Africa to fill the knowledge gaps necessary to implement the urgently required interventions. Both the small and declining population paradigms, and the ecological tools required to explain them, form the basis of this study in exploring and quantifying the decline of the Bearded Vulture population in southern Africa. The thesis is presented as a series of chapters written as stand-alone documents to facilitate publication. As such this has resulted in the use of the third person in Chapters 2-6 and the repetition of some information in the introduction and methods sections of these chapters.

Chapters 2-6 detail the results of data collected during 2000-2014. A schematic representation of the chapters is given in Figure 1.4.

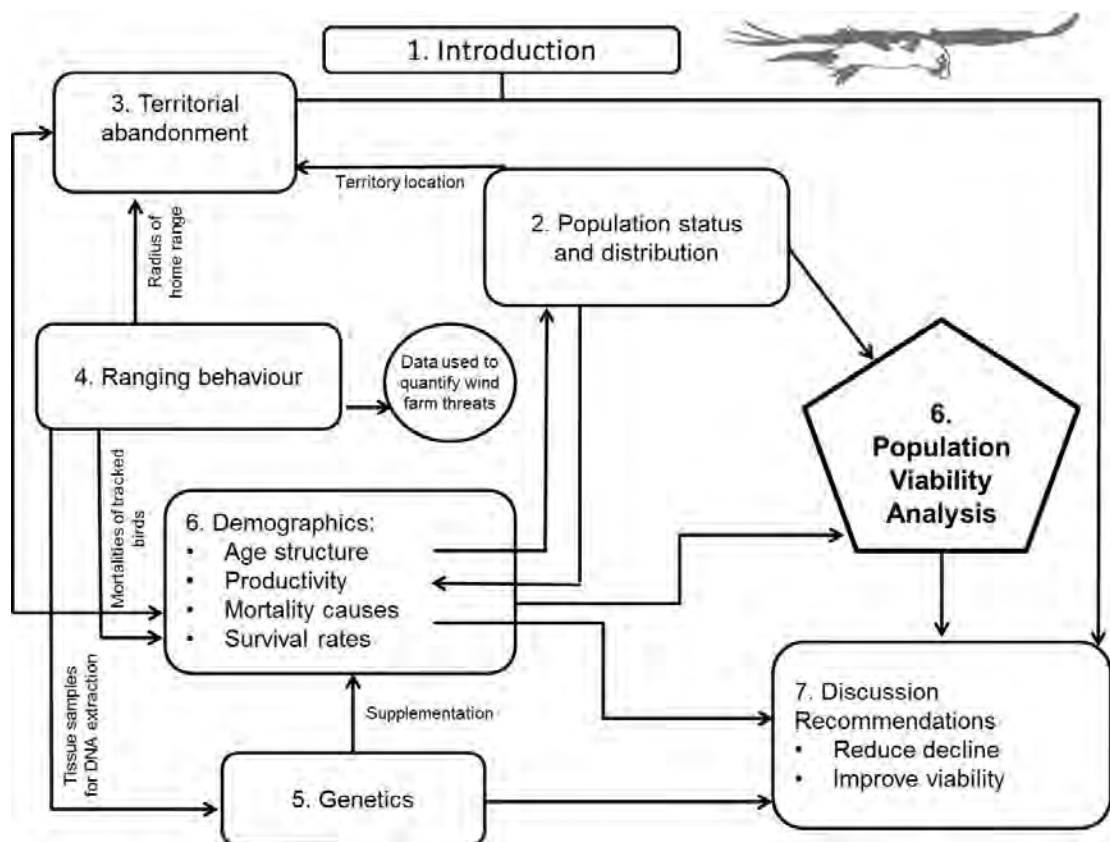


Figure 1.4 Schematic representation of the information provided in Chapters 1-7 indicating the flow of information between the chapters.

The first priority was to determine the current status and distribution of the population. Although *ad hoc* surveys had been conducted across the species' range, there had been no attempt at a population estimate since Brown's (1992) estimate of 608, extrapolated from his findings in parts of the range. My study represents the first attempt at a comprehensive survey of the entire breeding range of the species in southern Africa.

In Chapter 2, I investigate the breeding status, distribution and density of the Bearded Vulture in southern Africa and determine whether there has been a significant change in these parameters over the past 50 years. The chapter provides a recent population estimate which is critical for modelling population growth (Chapter 6). The information from annual surveys reported on in Chapter 2 provides the location and current status of all territories to investigate the mechanisms that have resulted in some territories being abandoned (Chapter 3). The bulk of Chapter 2 is published as a paper in Bird Conservation International (Krüger *et al.* 2014a).

Chapter 2 identified that many (at least 33%) of territories had been abandoned and were no longer occupied by breeding Bearded Vultures. I was therefore interested to know what factors might lead to the abandonment of these sites whilst other territories remained occupied. Thus, Chapter 3 explores whether the abandonment of territories was correlated with any key environmental variables which could shed light on the overall cause of the population's decline, similar to the methods used by Carrete *et al.* (2007) and Mateo-Tomás and Olea (2010) to investigate the causes of territory abandonment by the Endangered Egyptian Vulture *Neophron percnopterus*. Those variables found to influence territorial abandonment the most, need to be considered when formulating management recommendations (Chapter 7), together with an indication of direct threats from the causes of mortality (Chapter 6). The size of the area used to quantify environmental variables around the nest site, was obtained from estimates of adult home range size provided in Chapter 4.

In Chapter 4, I use data from GPS satellite tags fitted to birds of various age-classes to determine whether there are spatial and temporal differences in home-range use that places them at risk to certain anthropogenic factors, such as those driving the abandonment of breeding territories. Data on ranging behaviour of the species is limited to studies undertaken in Europe (Gil *et al.* 2010, Gil *et al. in press*, Margalida *et al.* 2013), or radio telemetry studies (Brown 1988) and studies on an individual juvenile (Urios *et al.* 2010) in southern Africa, which have limited application in determining age-specific home range size and the potential for risk exposure, causes of mortality and survival estimates for this population. In addition, data from this chapter has been used to inform wind turbine placement in the study area (Reid *et al. in review*). The mortalities of tagged individuals provided data on longevity, mortality rates and causes of mortality for modelling population growth (Chapter 6). The captured birds also provided an opportunity to collect tissue samples for genetic analyses (Chapter 5).

I investigate genetic risk in Chapter 5 as a potential threat to the population. Knowledge of the genetic variability and evolutionary placement of the local population will aid future management decisions on whether augmentation is required to increase genetic diversity in the population and to identify the source population for this purpose. Negro and Torres (1999) studied the genetic variability and placement of two populations of Bearded Vulture in Europe to inform reintroduction programmes, and others have looked at genetic variability in threatened (Poulakakis *et al.* 2008) and declining and fragmented populations (Martínez-Cruz *et al.* 2004) to inform management strategies. Whether augmentation (reintroductions) will assist population growth as well as improving diversity is investigated as a possible management scenario in Chapter 6. Chapter 5 has been published in Ibis (Krüger *et al.* 2014b).

Chapter 6 uses the current demographic information to i) model the population trend, ii) identify the key demographic parameters driving this trend, and iii) examine key interventions that can effectively influence this trend. Using this model I also tested whether I

could re-capitulate the observed history of the population trajectory from 1950 to 2000 based on current population estimates, survival rates and reproductive rates. This allowed me to explore whether changes in productivity or survival in isolation would have been sufficient to have caused the observed decline. Similar approaches were used successfully by Sarrazin *et al.* (2004) who explored the decline in vultures in South Asia and established that reduced productivity alone was insufficient to have driven the decline of that population.

The final chapter discusses the research findings detailed in Chapters 2-6 from work undertaken in southern Africa during 2000-2014, explores recommendations critical to the conservation of the Bearded Vulture population and prioritizes these based on their predicted impact. In so doing this study provides important information to fill many of the gaps identified in the BMP-S and provides the necessary guidance to achieve the aims for the regional population; that of a positive growth rate in the short term.

References

- African Development Bank Group (2012) African Development Bank Republic of South Africa Country Strategy Paper 2013-2017. Southern Africa Resource Centre (SARC) Department, *unpubl report*.
- African Development Bank Group (2013) African Development Bank Kingdom of Lesotho Country Strategy Paper 2013-2017. Southern Africa Resource Centre (SARC) Department, *unpubl report*.
- Allan DG and Jenkins AR (2005) Preliminary report on a survey of breeding sites of Bearded and Cape Vultures in Lesotho. Durban Natural Science Museum, Durban, *unpubl report*.

- Andelman SJ and Fagan WF (2000) Umbrellas and flagships: Efficient conservation surrogates or expensive mistakes? *Proc Nat Acad Sci USA* 97(11): 5254-5259.
- Anderson MD (2000) Bearded Vulture *Gypaetus barbatus*. In: Barnes KN (editor) The Eskom Red Data book of birds of South Africa, Lesotho and Swaziland. BirdLife South Africa, Johannesburg, pp. 39-41.
- Balmford A (1996) Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends Ecol Evol* 11: 193–196.
- BirdLife International (2001) Threatened Birds of Asia: the BirdLife International Red Data Book. BirdLife International, Cambridge.
- BirdLife International (2013) Spotlight on threatened birds. Presented as part of the BirdLife State of the world's birds website. Available from: <http://www.birdlife.org/datazone>.
- BirdLife International (2014) IUCN Red List for birds. Downloaded from <http://www.birdlife.org> on 05/08/2014.
- Boshoff AF, Brooke RK and Crowe TM (1978) Computerized distribution mapping scheme for vertebrates in southern Africa. *S Afr J Wildl Res* 8(4): 145-149.
- Branton M and Richardson JS (2011) Assessing the Value of the Umbrella-Species Concept for Conservation Planning with Meta-Analysis. *Conserv Biol* 25: 9–20. doi:10.1111/j.1523-1739.2010.01606.x.
- Brooke RK (1984) South African Red Data Book- Birds. *S Afr Nat Sci Prog Rep* 97. CSIR, Pretoria.
- Brown CJ (1988) A study of the Bearded Vulture *Gypaetus barbatus* in southern Africa. Dissertation, University of Natal, Pietermaritzburg.
- Brown CJ (1990) Breeding biology of the Bearded Vulture in southern Africa, Parts I – III. *Ostrich* 61: 24-49.

- Brown CJ (1991) An investigation into the decline of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Biol Conserv* 57: 315-337
- Brown CJ (1992) Distribution and status of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Ostrich* 63: 1-9.
- Brown CJ (1997) Population dynamics of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Afr J Ecol* 35: 53-63
- Bustamante J (1996) Population viability analysis of Captive and Released Bearded Vulture Populations. *Conserv Biol* 10(3): 822-831.
- Butchart SHM *et al.* (2010) Global Biodiversity: Indicators of Recent Declines. *Science* 328: 1164.
- Carrete M, Grande JM, Tella JL, Sánchez-Zapata JA, Donazar JA, Díaz-Delgado R and Romo A (2007) Habitat, human pressure, and social behavior: partialling out factors affecting large-scale territory extinction in an endangered vulture. *Biol Conserv* 136(1): 143-154.
- Caughley G (1994) Directions in Conservation Biology. *J Anim Ecol* 63: 215–244. doi:102307/5542.
- Channell R (2004) The Conservation Value of Peripheral Populations: the Supporting Science. In: Hooper TD (editor) Proceedings of the Species at Risk 2004 Pathways to Recovery Conference. 1 March 2–6, 2004, Victoria, B.C.
- Cortez-Avazida A, Carrete M and Donazar JA (2010) Managing supplementary feeding for avian scavengers: guidelines for optimal design using ecological criteria. *Biol Conserv* 143: 1707-1715.
- Cramp S and Simmons KEL (1980) Handbook of the Birds of Europe, the Middle East and North Africa. Oxford University Press, Oxford.

- DeVault TL., Brisbin IL and Rhodes OE (2004) Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers. *Can J of Zool* 82: 502–509.
- Dirzo R, Young HS, Galetti M, Ceballos, G Isaac NJB and Collen B (2014) Defaunation in the Anthropocene. *Science* 345: 401. doi:10.1126/science.1251817.
- Donázar JA, Margalida A, Carrete M and Sánchez-Zapata JA (2009) Too sanitary for vultures. *Science* 326(5953): 664.
- Ferguson-Lees J and Christie DA (2001) Raptors of the world. Christopher Helm, London.
- Fleishman E *et al.* (2011) Top 40 Priorities for Science to Inform US Conservation and Management Policy. *Biosci* 61(4): 290-300.
- García CB, Insausti JA, Gil JA, de Frutos A, Alcántara M, González J, Cortés MR, Bonafonte JI and Arruga MV (2009) Comparison of different procedures of DNA analysis for sex identification in the endangered bearded vulture (*Gypaetus barbatus*). *Eur J Wildl Res* 55(3): 309-312.
- Gil JA, Díez O, Báguena G, Lorente L, Pérez C, Losada JA and Alcántara M (2010) Juvenile dispersal of the bearded vulture (*Gypaetus barbatus*) in the Pyrenees (Spain-France). Fundación para la Conservación del Quebrantahuesos (FQC), Spain.
- Gil JA, Báguena G, Sánchez-Castilla E, Antor RJ, Alcantara M and Lopéz-Lopéz P (*in press*) Home-range and movements of non-breeding bearded vultures tracked by satellite telemetry in the Pyrenees. *Ardeola*.
- Godoy JA, Negro JJ, Hiraldo F and Donázar JA (2004) Phylogeography, genetic structure and diversity in the endangered bearded vulture (*Gypaetus barbatus*, L.) as revealed by mitochondrial DNA. *Mol Ecol* 13: 371-390.
- Green RE (1995) Diagnosing the causes of bird population declines. *Ibis* 137: S47–S55.

- Green RE (2002) Diagnosing causes of population declines and selecting remedial actions. In: Norris K and Pain DJ (editors) *Conserving Bird Biodiversity*. Cambridge University Press, Cambridge, UK, pp. 139–156.
- Green RE, Newton I, Schultz S, Cunningham AA, Gilbert M, Pain DJ and Prakash V (2004) Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. *J Appl Ecol* 41: 793–800.
- Hedrick PW, Lacy RC, Allendorf FW and Soule ME (1996) Directions in conservation biology: comments on Caughley. *Conserv Biol* 10: 1312–1320.
- Heredia R (1991) Chapter 2 Biología de la Reproducción. In: Heredia R and Heredia B (editors) *El Quebrantahuesos (*Gypaetus barbatus*) en los Pirineos*. ICONA, Madrid.
- Heredia R and Heredia B (1999) *El Quebrantahuesos *Gypaetus barbatus* en los Pirineos: características ecológicas y biología de la conservación*. The Bearded Vulture in the Pyrenees: ecology and conservation biology. Colección Técnica. ICONA, Madrid.
- Herremans M and Herremans-Tonnoyer D (2000) Land use and the conservation status of raptors in Botswana. *Biol Conserv* 94: 31–41.
- Hiraldo F, Delibes M and Calderon J (1979) *El Quebrantahuesos: sistemática, taxonomía, biología, distribución y protección*. Monografías 22, ICONA, Madrid.
- Hiraldo F, Delibes M and Calderón J (1984) Comments on the taxonomy of the bearded vulture *Gypaetus barbatus* (Linnaeus, 1758). *Bonn Zool Beitr* 35: 91–95.
- Hirzel AH, Posse B, Oggier P, Crettenand Y, Glenz C and Arlettaz R (2004) Ecological requirements of reintroduced species and the implications for release policy: the case of the bearded vulture. *J Appl Ecol* 41: 1103–1116.
- Hoffmann M *et al.* (2010) The impact of conservation on the status of the world's vertebrates. *Science* 330: 1503–1509.

- Houston DC and Cooper JE (1975) The digestive tract of the Whiteback Griffon Vulture and its role in disease transmission among wild ungulates. *J Wildl Dis* 11: 306–313.
- Isasi-Catala E (2011) Indicator, umbrellas, flagships and key-stone species concepts: Use and abuse in conservation ecology. *Interciencia* 36: 31-38.
- Jamshed J, Chaudhry I, Ogada DL, Malik RN, Virani MZ and Giovanni MD (2012). First evidence that populations of the critically endangered Long-billed Vulture *Gyps indicus* in Pakistan have increased following the ban of the toxic veterinary drug diclofenac in south Asia. *Bird Conserv Int* 22(4): 389-397. doi:10.1017/S0959270912000445.
- Keller LF and Waller DM (2002) Inbreeding effects in wild populations. *Trends Ecol Evol* 17: 230–241.
- Kissui BM (2008) Livestock predation by lions, leopards and spotted hyaenas, and their vulnerability to retaliatory killing in the Masai steppe, Tanzania. *Anim Conserv* 11: 422-432.
- Koenig R (2006) Vulture Research Soars as the Scavengers' Numbers Decline. *Science* 312: 1591-1592.
- Krüger S (2006) The 2005 Bearded Vulture (*Gypaetus barbatus meridionalis*) Ground Survey, South Africa. Ezemvelo KZN Wildlife, *unpubl report*.
- Krüger S (editor) (2013) Biodiversity Management Plan for the Bearded Vulture (*Gypaetus barbatus meridionalis*) for Southern Africa. Published 8 May 2014 Government Gazette Notice No 37620.

- Krüger S, Piper S, Rushworth I, Botha A, Daly B, Allan D, Jenkins A, Burden D and Friedmann Y (editors) (2006) Bearded Vulture (*Gypaetus barbatus meridionalis*) Population and Habitat Viability Assessment Workshop Report. Conservation Breeding Specialist Group (SSC/IUCN)/CBSG Southern Africa, Endangered Wildlife Trust, Johannesburg.
- Krüger SC, Allan DG, Jenkins AR and Amar A (2014a) Trends in territory occupancy, distribution and density of the Bearded Vulture *Gypaetus barbatus meridionalis* in southern Africa. *Bird Conserv Int* 24: 162-177. doi:10.1017/S0959270913000440.
- Krüger SC, Wesche PL and Jansen van Vuuren B (2014b) Reduced genetic diversity in Bearded Vultures *Gypaetus barbatus* in Southern Africa. doi: 10.1111/ibi.12200.
- Lipiya A (2011) Status of Birds of Prey, with Special Emphasis on Vultures, in Kasungu National Park. Department of National Parks and Wildlife, Lilongwe *unpubl report*, 5pp.
- Lindenmayer DB, Manning AD, Smith PL, Possingham HP, Fischer J, Oliver I and McCarthy MA (2002) The Focal-Species Approach and Landscape Restoration: a Critique. *Conserv Biol* 16(2): 338–345.
- Lomolino MV and Channell R (1995) Splendid isolation: patterns of range collapse in endangered mammals. (special feature in biogeography). *J Mammal* 76: 335–347.
- Lomolino MV and Perault DR (1998) Patterns of geographic range collapse in endangered species. Society of Conservation Biologists meeting *unpubl report*, Victoria, BC.
- Madsen T, Shine R, Olsson M and Wittzell H (1999) Restoration of an inbred adder population. *Nature* 402: 34–35.

- Mander M, Diederichs N, Ntuli L, Khulile M, Williams V and McKean S (2007) Survey of the Trade in Vultures for the Traditional Health Industry in South Africa. Futureworks, *unpubl report*, 30pp
- Margalida A, García D and Cortés–Avizanda A (2007) Factors influencing the breeding density of Bearded Vultures, Egyptian Vultures and Eurasian Griffon Vultures in Catalonia (NE Spain): management implications. *Anim Biodiv Conserv* 30(2): 189–200.
- Margalida A, Carrete M, Hegglin D, Serrano D, Arenas R and Donazar JA (2013) Uneven Large-Scale Movement Patterns in Wild and Reintroduced Pre-Adult Bearded Vultures: Conservation Implications. *PLoS ONE* 8(6): e65857. doi:10.1371/journal.pone.0065857.
- Markandya A, Taylor T and Longo A (2008) Counting the cost of vulture decline—an appraisal of the human health and other benefits of vultures in India. *Ecol Econ* 67: 194–204.
- Martínez-Cruz B, Godoy JA and Negro JJ (2004) Population genetics after fragmentation: the case of the endangered Spanish imperial eagle (*Aquila adalberti*). *Mol Ecol* 13: 2243–2255.
- Mateo-Tomás P and Olea PP (2010) Diagnosing the causes of territory abandonment by the Endangered Egyptian vulture *Neophron percnopterus*: the importance of traditional pastoralism and regional conservation. *Oryx* 44: 424–433.
- McLachlan JS, Hellmann JJ and Schwartz MW (2007) A framework for debate of assisted migration in an era of climate change. *Conserv Biol* 21: 297–302.
- Meffe GK and Carroll CR (1994) Principles of Conservation Biology. Sinauer, Sunderland, MA.

- Mingozzi T and Estève R (1997) Analysis of a historical extirpation of the Bearded vulture *Gypaetus barbatus* (L) in the Western Alps (France-Italy): former distribution and causes of extirpation. *Biol Conserv* 79: 155-171.
- Mundy P, Butchart D, Ledger J and Piper S (1992) The Vultures of Africa. Russel Friedman Books CC, Johannesburg, South Africa.
- Naeem S and Wright JP (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecol Lett* 6: 567–579.
- Negro JJ and Torres MJ (1999) Genetic variability and differentiation of two bearded vulture *Gypaetus barbatus* populations and implications for reintroduction projects. *Biol Conserv* 87: 249–254.
- Newmark WD, Manyanza DN, Gamassa D-GM and Sariko HI (1994) The conflict between wildlife and local people living adjacent to protected areas in Tanzania: human density as a predictor. *Conserv Biol* 8: 249-255.
- Norris K (2004) Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *J Appl Ecol* 41: 413–426.
- Oaks *et al.* (2004) Diclofenac residues as the cause of vulture population decline in Pakistan. *Nature* 427: 630-633.
- Ogada DL (2014) The power of poison: pesticide poisoning of Africa's Wildlife. *Ann NY Acad Sci*. doi:10.1111/nyas.12405.
- Ogada DL, Torchin ME, Kinnaird MF and Ezenwa VO (2011) Effects of Vulture Declines on Facultative Scavengers and Potential Implications for Mammalian Disease Transmission. *Conserv Biol* 26(3): 453–460.
- Ogada DL, Keesing F and Virani MZ (2012) Dropping dead: causes and consequences of vulture population declines worldwide. *Ann NY Acad Sci* 1249: 57-71.

- Ogden J (1985) The California Condor In: Silvestro RL (editor) Audubon wildlife report 1985 National Audobon Society, New York, pp. 389-99.
- Pain DJ, Cunningham AA and Donald PF 2003. Causes and effects of temporospatial declines of *Gyps* vultures in Asia. *Conserv Biol* 17: 661–671.
- Pain DJ *et al.* (2008) The race to prevent the extinction of South Asian vultures. *Bird Conserv Int* 18: S30–S48. doi: 10.1017/S0959270908000324.
- Parmesan C and Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.
- Poulakakis N, Antoniou A, Mantziou G, Parmakelis A, Skartsi T, Vasilakis D, Elorriaga J, de la Puente J, Gavashelishvili A, Ghasabyan M, Katzner T, McGrady M, Batbayar N, Fuller M and Natsagdorj T (2008) Population structure, diversity, and phylogeography in the near-threatened Eurasian black vultures *Aegypius monachus* (Falconiformes; Accipitridae) in Europe: insights from microsatellite and mitochondrial DNA variation. *Biol J Linn Soc* 95: 859–872.
- Pimm SL, Jones HL and Diamond J (1988) On the risk of extinction. *Am Nat* 132: 757-785.
- Reid T, Krüger S, Whitfield P and Amar A (*in review*) Using spatial analyses of bearded vulture movements in southern Africa to inform wind turbine placement.
- Roberge J-M and Angelstam P (2004) Usefulness of the Umbrella Species Concept as a Conservation Tool. *Conserv Biol* 18(1): 76–85.
- Roxburgh L and McDoughall R (2012) Vulture poisoning incidents and the status of vultures in Zambia and Malawi. *Vulture News* 62: 33-39.

- Sarrazin F, Virani MZ, Gilbert M and Khan A (2004) Preliminary Population Viability Analyses for Oriental White-Backed Vulture *Gyps bengalensis* in Punjab province, Pakistan. In: Chancellor RD and Meyburg BU (editors) *Raptors Worldwide*. WWGBP & MME Penti Kft, Budapest, pp. 257–262.
- Schaub M, Zink R, Beissmann H, Sarrazin F and Arlettaz R (2009) When to end releases in reintroduction programmes: demographic rates and population viability analysis of bearded vultures in the Alps. *J Appl Ecol* 46: 92–100. doi: 10.1111/j.1365-2664.2008.01585.x
- Seddon PJ, Griffiths CJ, Soorae PS and Armstrong DP (2014) Reversing defaunation: Restoring species in a changing world. *Science* 345(6195): 406-412.
- Sekercioglu CH, Daily GC and Ehrlich PR (2004) Ecosystem consequences of bird declines. *Proc Nat Acad Sci* 101: 18042–18047.
- Shrader-Frechette KS and McCoy ED (1993) *Method in Ecology. Strategies for Conservation*. Cambridge University Press, Cambridge.
- Siegfried WR, Frost PGH, Cooper J and Kemp AC (1976) Rare and vulnerable birds in South Africa. *Biol Conserv* 10: 83–93.
- Simberloff D (1997) Invasion biology and Florida's numerous non-indigenous species. In: Simberloff D, Schmitz DC and Brown TC (editors) *Strangers in Paradise. Impact and Management of Non-indigenous Species in Florida*. Island Press, Washington DC, pp. 3-17.
- Sutherland WJ *et al.* (2011) Horizon scan of global conservation issues for 2011. *Trends Ecol Evol* 26(1): 10-16.
- Sycholt A (2002) *A guide to the Drakensberg*. Struik Publishers, Cape Town, South Africa.
- Thiollay J-M (2006) The decline of raptors in West Africa: long-term assessment and the role of protected areas *Ibis* 148: 240–254.

- Thomas CD *et al.* (2004) Extinction risk from climate change. *Nature* 427: 145–148.
- Tracy CR and Brussard PF (1994) Preserving biodiversity: species in landscapes. *Ecol App* 142: 205-207.
- UN Environment Programme (2007) Global Environmental Outlook: Environment for Development 4. United Nations Environment Programme, Valletta.
- Urios V, López-López P, Limiñana R and Godino A (2010) Ranging behaviour of a juvenile Bearded Vulture (*Gypaetus barbatus meridionalis*) in South Africa revealed by GPS satellite telemetry. *Ornis Fenn* 87: 1-5.
- Vignieri S (2014) Vanishing fauna. *Science* 354(6195): 392-395:
- Virani MZ, Kendall C, Njoroge P and Thomsett S (2011) Major declines in the abundance of vultures and other scavenging raptors in and around the Masai Mara ecosystem, Kenya. *Biol Conserv* 144: 746-752.
- Watts HE and Holekamp KE 2009. Ecological determinants of survival and reproduction in the spotted hyaena. *J Mammal*. 90: 461-471.
- Whitley A (1998) Modelling the distribution of vultures in KwaZulu-Natal, South Africa in relation to environmental variables. Dissertation, University of Natal, Pietermaritzburg.
- Woodroffe R (2000) Predators and people: using human densities to interpret declines of large carnivores *Anim Conserv* 3: 165–173.
- Woodroffe R and Ginsberg JR (1998). Edge effects and the extinction of populations inside protected areas. *Science* 280: 2126–2128.

Publications arising from this thesis

In all cases I have lead and conducted the field and laboratory work, data analysis and write-up. Co-authors of the chapters assisted with data analyses (Chapters 2-6) and laboratory work (Chapter 5). Co-authors (listed by chapter below) and my supervisors (Dr Arjun Amar and Dr Rob Simmons) assisted with revisions to the manuscripts. All other assistance received has been acknowledged either where relevant in each chapter or in the general acknowledgements preceding the introduction.

Chapter 2 is published in Bird Conservation International:

Krüger SC, Allan DG, Jenkins AR and Amar A (2014) Trends in territory occupancy, distribution and density of the Bearded Vulture *Gypaetus barbatus meridionalis* in southern Africa. *Bird Conserv Int* 24: 162-177. doi:10.1017/S0959270913000440.

Chapter 3 has been accepted by The Condor and is in press:

Krüger SC, Simmons RE and Amar A (*in review*) Anthropogenic activities influence the abandonment of Bearded Vulture *Gypaetus barbatus* territories in southern Africa.

Chapter 4 has been accepted by PLoS ONE and is in press:

Krüger SC, Reid T and Amar A (*in review*) Differential range use between age classes of southern African Bearded Vultures *Gypaetus barbatus*.

Chapter 5 is published online in Ibis:

Krüger SC, Wesche PL and Jansen van Vuuren' B (2014) Reduced genetic diversity in Bearded Vultures *Gypaetus barbatus* in Southern Africa. doi: 10.1111/ibi.12200.

Chapter 6 will be submitted to Oryx.

Krüger SC and Amar A. Poisoning increases the extinction risk of the Bearded Vulture *Gypaetus barbatus* in southern Africa.

Additional relevant publications arising from this research include the following:

Krüger SC (2007) Polyandrous trios in the southern African Bearded Vulture *Gypaetus barbatus meridionalis*? *Vulture News* 57:60-61.

Krüger S (editor) (2013) Biodiversity Management Plan for the Bearded Vulture (*Gypaetus barbatus meridionalis*) for Southern Africa. Published 8 May 2014 Government Gazette Notice No 37620.

Krüger S (*in press*). Bearded Vulture. In: Taylor MR (editor) The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. BirdLife South Africa, Johannesburg.

Krüger S, Piper S, Rushworth I, Botha A, Daly B, Allan D, Jenkins A, Burden D and Friedmann Y (editors) (2006) Bearded Vulture (*Gypaetus barbatus meridionalis*) Population and Habitat Viability Assessment Workshop Report. Conservation Breeding Specialist Group (SSC/IUCN)/CBSG Southern Africa, Endangered Wildlife Trust, Johannesburg.

Reid T, **Krüger S**, Whitfield P and Amar A (*in review*) Using spatial analyses of bearded vulture movements in southern Africa to inform wind turbine placement (submitted to *J Appl Ecol*).

Rushworth I and **Krüger S** (2014) Wind farms threaten southern Africa's cliff-nesting vultures, *Ostrich* 85(1): 13-23. doi:10.2989/00306525.2014.913211.

Chapter 2: Trends in territory occupancy, distribution and density of the Bearded Vulture *Gypaetus barbatus* in southern Africa



Photo 2 Adult Bearded Vulture seen on a nest during a breeding territory survey

A modified form of this chapter is published in Bird Conservation International:

Krüger SC, Allan DG, Jenkins AR and Amar A (2014) Trends in territory occupancy, distribution and density of the Bearded Vulture *Gypaetus barbatus meridionalis* in southern Africa. *Bird Conserv Int* 24: 162-177. doi:10.1017/S0959270913000440.

Abstract

Territory occupancy, distribution and density of the isolated Bearded Vulture *Gypaetus barbatus* population in the Maloti-Drakensberg mountains of southern Africa were assessed between two time periods - former (1960-1999) and current (2000-2012) - to identify population trends. Overall, 190 territories were recorded of which 109 are currently occupied. The number of occupied breeding territories decreased by a minimum of 32% and a maximum of 51% over the past five decades representing an unequivocal decline in this population at a rate of between 0.64-1.02% per year. The encounter rate of individuals during vehicle surveys also decreased by 45% over a 30 year time period. Territories located on the periphery of the breeding range were more likely to be abandoned than those in the core. The current population is estimated at a minimum of 368 and a maximum of 408 individuals. The breeding range decreased by 27%, restricting the birds to an estimated area of occupancy of 28,125 km². Breeding densities also decreased by 20%, declining from 4.9 to 3.9 pairs/1000 km². In both periods, higher densities were recorded in the core of the range. Nests were located about 9.0 km apart, a slight increase from the 7.7 km recorded formerly. Inter-nest distances increased with distance from the core of the range. Further studies are required to ascertain whether productivity or survival is limiting population growth, and whether anthropogenic influences are resulting in the abandonment of territories in the periphery of the range and the subsequent decline in numbers.

Introduction

Vulture populations are declining worldwide (BirdLife International 2014). In Africa, large reductions in vulture numbers have occurred in recent decades in areas where these birds were previously abundant, to the extent that some populations have either become locally extinct or are found only in protected areas (Ogada *et al.* 2012). In keeping with these trends, Bearded Vulture *Gypaetus barbatus* populations are declining throughout much of the species' range (Margalida *et al.* 2008a, BirdLife International 2014), and have been since as early as the mid-

19th century, with some populations nearing extinction by the mid-20th century (Mingozzi and Estève 1997).

Two distinct subspecies of Bearded Vulture are recognized. The subspecies *G. b. barbatus* occurs north of the Tropic of Cancer in Asia, Europe and North Africa, while *G. b. meridionalis* occurs south of Tropic of Cancer in Ethiopia, East Africa and southern Africa (Mundy *et al.* 1992). Globally, the species is classified as Near Threatened (BirdLife International 2014). Although the global population size is small and seems to be decreasing, the species has a very large range and the overall decrease in numbers is not rapid enough to justify its classification as Vulnerable. However, a number of discrete sub-populations within each of the two subspecies are threatened with extinction and our aim here is to quantify the decline for the southern African subspecies.

In central Asia and the Himalayas, Bearded Vultures seem abundant (Terrasse 2001), although significant declines have been noted recently in the Upper Mustang region of Nepal (Acharya *et al.* 2010). Numbers have also decreased further west, with recent localised extinctions in the Mediterranean, mainly attributed to human persecution and poisoning (Frey 1996, Xirouchakis *et al.* 2001). In Europe, the species has disappeared from many parts of its historical distribution (Hiraldo *et al.* 1979, Del Hoyo *et al.* 1994, Frey 1996, Mingozzi and Estève 1997, Carrete *et al.* 2006, Margalida *et al.* 2008a), and it is now considered Endangered in the European Union (Annex I, EU Wild Birds Directive 79/409/EEC, Appendix II of the Bern Convention, Bonn Convention and CITES). The North African population of *G. b. barbatus* remains small and isolated from other Mediterranean populations, with a high risk of extinction in the medium-to-long term (Godino *et al.* 2005).

Within sub-Saharan Africa, knowledge of the species is poor. Earlier, crude estimates of the numbers of pairs of *G. b. meridionalis* in Ethiopia and East Africa were 1,430 and 50 respectively (Mundy *et al.* 1992), while the most recent published report puts the East African population at only 20-30 pairs (Zimmerman *et al.* 1996). More recent, unpublished reports

suggest that the number of pairs in Ethiopia and East Africa is significantly lower than these previous estimates, particularly in East Africa where apparently only about 10 pairs remain (S. Thomsett *pers. comm.*). Other reports from Ethiopia also suggest a decrease (Ash and Atkins 2009), but basic data on population status is lacking from this country (Shimelis 2011).

In southern Africa, the population lost *ca.* 38% of its former distribution range during the period 1700-1969 (Boshoff *et al.* 1978, 1983, Brooke 1984, Brown 1991) and was described as “rare and threatened” in a review of the status of threatened South African birds in the 1970s (Siegfried *et al.* 1976). The population continued to decline in the 1970s and 1980s although the distribution remained constant (Brown 1991). The extent of the breeding range of the Bearded Vulture in southern Africa was estimated to be about 35,000 km² during 1980-1983, a reduction of 21,000 km² from the historic distribution which extended into the south-western Cape (Brown 1991), with the population largely restricted to the highlands of Lesotho and immediately adjacent areas of the Maloti-Drakensberg mountains (Brown 1990). In the 1980s, the breeding population was estimated at 204 pairs based on extrapolations from 61 known breeding territories (Brown 1992). The breeding density ranged from 3.4-7.2 pairs/1000 km² in the seven geographical regions used by Brown (1992) to estimate density. In the 1990s, Colahan and Esterhuizen (1997) observed no breeding pairs in the Free State, and Maphisa (1997) noted that sightings in the lowlands of Lesotho were rare and that some breeding territories were abandoned. In 2000, the Bearded Vulture was classified as Endangered in the red data book of birds of South Africa, Lesotho and Swaziland (Anderson 2000a), as a result of its small and continuously declining population size, restricted range, range contraction, and its susceptibility to several known threats in Lesotho and South Africa.

A more recent review of the conservation status of the Bearded Vulture in southern Africa (Krüger *et al.* 2006) indicated that numbers were continuing to decrease. However, the review also identified the lack of sufficient knowledge and understanding of the basic demography of the regional population as a major deficiency, and an urgent need to accurately

determine the number and distribution of breeding pairs and the causes of current trends in the occupancy of breeding territories.

Bird population declines can show a number of patterns; for example, populations can exhibit range contraction alone, range contraction and reduced densities in marginal and/or optimal habitat, or no range contraction but reduced densities (Wilcove and Terborgh 1984). Declining populations may abandon marginal habitats or peripheral areas and contract toward the core of the species' range (Mayfield 1972, 1973a, 1973b, Rodríguez 2002), or they may show reduced densities in the periphery of the range (Wilcove and Terborgh 1984). Understanding the pattern of decline, may help to infer the causes of the decline which will aid the development of appropriate monitoring and conservation measures.

In this chapter, we use data from 13 years of ground and aerial surveys of the Bearded Vulture population in southern Africa to document the number and location of breeding territories as a measure of population size, and thereby estimate the size of the species' breeding range and its breeding density. We also compare our numbers with those derived from a collation of historical survey data (1960-1999), to establish and explain the extent and pattern of decline shown by the southern African Bearded Vulture population over recent decades. In particular, we explore whether the southern African Bearded Vulture population has shown a change in territory occupancy, distribution and density over the two survey periods, and then examine whether this change has been more pronounced in the periphery of their breeding range. This chapter aims to improve our understanding of the current dynamics of the region's Bearded Vulture population, and to help produce more accurate population projections in Chapter 6 to guide *in situ* conservation decisions.

Methods

Census of Former and Current Breeding Territories

The location of former breeding territories (defined as cliffs that have a history of use by nesting Bearded Vulture) was obtained from a variety of published records and unpublished reports (Appendix 2.1). These documents included details of all known breeding territories occupied since the 1960s- the earliest records of nest site locations within the breeding distribution range in the Maloti-Drakensberg mountains (Brown 1992). A similar approach was used by Whitfield *et al.* (2006) to classify all potential territories of Golden Eagles *Aquila chrysaetos* in Scotland.

We then attempted to determine the current occupancy status of these breeding territories, and to identify any additional territories that may have remained undiscovered, through extensive ground and aerial helicopter surveys conducted between 2000-2012. Potential new territories were identified from topographical maps, by land managers from a questionnaire survey conducted within the species' range (Hiltunen 2008) and from individuals who had carried out other field-based activities in specific localities of interest. We then surveyed these potential territories to confirm their occupancy status. Our 13-year census period with multiple visits to most sites (Appendix 2.2a: 77% of sites visited more than once) gave us the confidence that observed trends were real and not a result of year-to-year population fluctuations or survey and observer biases.

Full details of the census method followed between 2000-2012 are available in Brown (1992) but are described briefly below. Surveys were undertaken during the breeding period (nest building to fledging: May to December) because fidelity to nest sites is highest during this period which increased the probability of seeing birds with territorial behaviour (*i.e.* nest-building, nest defence) and determining the occupancy status of the territory. Ground surveys were done on foot or by vehicle, and potential breeding territories were scanned using binoculars and 20-60 X telescopes for an average of four hours (4.24 ± 0.18 hours, $n=122$,

range 0.5-11.5 hours) between first and last light, or until breeding was confirmed. Bearded Vulture pairs are known to have a number of alternate nests on average 230 m apart (Brown 1988), therefore observations included all the cliff faces containing all potential alternate nests of that territory. To ensure that the observation period was sufficient, surveys were predominantly (69%, n=608) done during the nestling period when activity at the nest peaks, with either an attendant adult or with food being provisioned several times a day (Brown 1990). Since territories recorded by Brown (1990) were on average 7.2 km apart, observers were able to distinguish between neighbouring territories.

Aerial surveys were done in helicopters, flown at approximately 100-500 m from the cliff edge at an average flying speed of 70-80 km/h with a minimum of two observers looking out of the port side of the aircraft. The census method followed between 1960-1999 included a variety of protocols including those of Brown (1992) described above (Appendix 2.2b).

Territories were considered *occupied* if at least one adult was flushed off the cliff or seen flying or roosting in the area, entering a pothole or overhang on the cliff; if a chick or fledgling was seen; or if there was fresh whitewash and plant material (sticks) on the nest indicating recent use attributed to this species based on the location of the white-wash and the type of nest structure. Where nest structures were seen but no bird was seen in the area, the territory was recorded as *unoccupied*. Nest structures can remain intact in potholes long after abandonment, therefore nest structures alone do not serve as a useful indicator of occupancy. Territories where nest structures were no longer evident or where birds had not been seen in a number of years (at least four consecutive years of survey) were considered *abandoned*.

The location of all territories was entered into the geographic information system, ArcGIS v.9.3 (ESRI, Redlands, USA). Since the GPS coordinates recorded were those of the aircraft or the observer on the ground and not of the nest, the actual location of the nest site was extrapolated to the cliff edge. Where a pair had alternate nest sites on the territorial cliff, the location of the most frequently used site was taken as the location of the territory. As a means of

examining regional patterns of change, breeding territories were grouped and compared by country and district (Lesotho) or province (South Africa) (Figure 2.1).

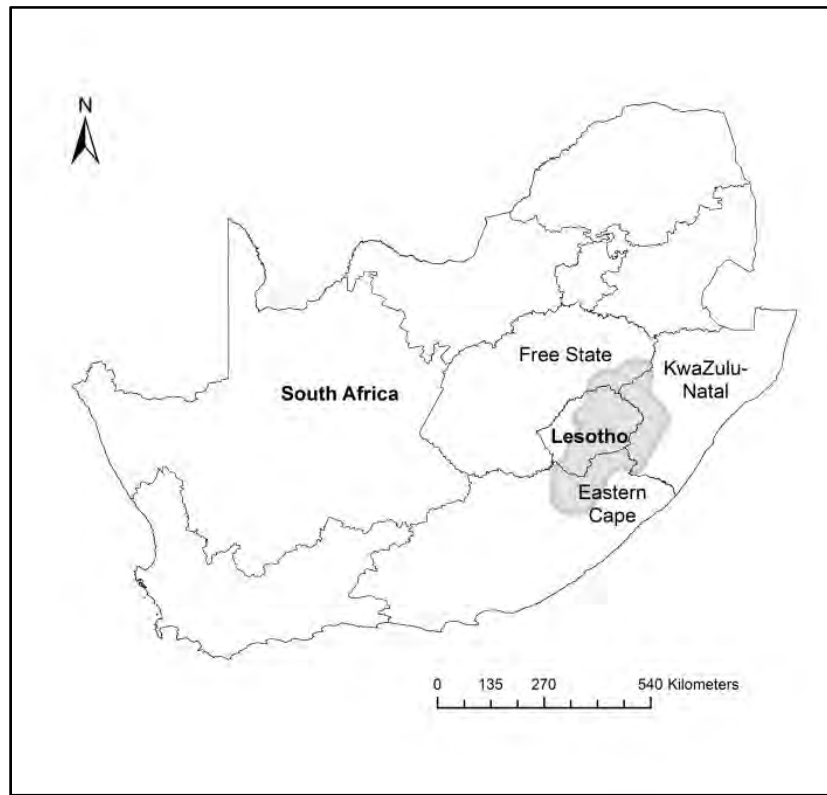


Figure 2.1 The location of the southern African distribution range of the Bearded Vulture within Lesotho and the three provinces of South Africa.

Estimating Territory Occupancy and Population Size

We compared current (territories occupied during 2000-2012) and former (territories occupied during 1960-1999) territory occupancy using two scenarios. Firstly, we calculated population change based on the current status of all territories recorded during 1960-1999. This scenario excluded those territories recorded for the first time during 2000-2012 and therefore represents the minimum population change. For this calculation, we took into account that a pair may have moved their breeding activity to a nearby cliff between the former and current study period, rather than abandoning their territory. Our decision to categorise whether a pair had abandoned or potentially relocated their territory was based on the status of, and distance to, the neighbouring breeding territory within that time period. We used Brown's (1990) estimate of

maximum average inter-nest distance (7.2 km) as the deciding factor; where 'abandoned' former nests located <7.2 km from current nests were considered to be nest relocations within the same territory, while those located >7.2 km from any current nests were considered to have been abandoned. Territories where former occupied nests were located <7.2 km of each other were considered abandoned rather than relocated if the neighbouring territory was still occupied.

Secondly, we assumed that all territories located for the first time during the current survey period (2000-2012) were occupied formerly (1960-1999) based on the knowledge that pairs use alternate nests on the same cliff rather than moving to a different cliff (Brown 1990), and many territories had large, well established nest structures suggesting many years of use. All known territories were considered occupied at some point since 1960 and therefore represented potential breeding territories. If all potential territories were occupied in any one year this would represent the total overall potential former population size. However it is unlikely that all territories would be occupied annually. Therefore, when examining population change we are reporting on maximum population change, since all territories would not necessarily have been occupied every year between 1960-1999 and 2000-2012.

Territory occupancy data were used to estimate the minimum and maximum number of Bearded Vultures in southern Africa. The total number of currently occupied territories together with the total number of known trios were used to calculate the number of breeding adults in the population. Estimates of non-breeding adults are not available for the population and are difficult to ascertain (Margalida *et al.* 2011). It was assumed that there were no non-breeding adults in the population based on Brown (1997) and personal observations of slow replacement at territories where an individual of a pair had disappeared. To estimate population size, we used the age ratio (adults : non-adults) calculated from foot surveys done in the core breeding range and vehicle surveys done throughout the range (see Chapter 6 for details).

Estimating Breeding Distribution and Density

The extent of the former and current breeding range was measured by Minimum Convex Polygons using the Hawth's analysis tools (Beyer 2004) for ArcGIS. The area of occupancy of the former and current population was measured using the distribution of occupied breeding territories within quarter degree squares (QDSs), making it comparable with Brown's (1992) study. The number of occupied QDSs was multiplied by the size of a QDS (625 km²) to obtain the area of occupancy.

Breeding density was examined using the number of breeding pairs per 1000 km² based on the area of occupancy. Inter-nest distances were measured as the distance to the nearest nest of a neighbouring conspecific pair.

Estimating Encounter Rates

To examine the change in the relative abundance of adults and non-adults in the study area over the past 30 years, data from vehicle surveys undertaken in 2012 across the range were compared with data collected along the same routes in 1981 by Brown (1988, 1992). Vehicle surveys were conducted following the method of Brown (1992) and the following were recorded; bird numbers and ages, distance travelled and duration of survey. The average speed of travel during vehicle surveys was 20 km/h. A total of 2,231 km of vehicle surveys were driven; 816 km in July in the Lesotho highlands west of the Senqu River, 799 km in September in Lesotho east of the Senqu River, and 616 km in December in the northern part of the Eastern Cape (see Figure 6.1, Chapter 6).

Core versus Peripheral Territories

Territories were classified as either within the core breeding range or the peripheral breeding range based on the number of surrounding QDSs that contained occupied breeding territories.

Territories were classified as 'Peripheral' if they were surrounded by four or less QDSs (giving an index of between 0-4) that contained occupied breeding territories. 'Core' territories were those surrounded by at least five occupied QDSs (giving an index of between 5-8).

Statistical Analyses

We used a Generalized Linear Model (GLiM) with a binomial distribution to examine territory status in relation to country (South Africa or Lesotho), which was fitted as a categorical effect. We used a General Linear Model (GLM) (*i.e.* with a normal distribution) to examine inter-nest distances in relation to period (former or current) and location (core or periphery), which were fitted as categorical effects. We tested whether the probability of a territory being occupied or abandoned differed depending on the level of its periphery index. For this we used a GLiM (binomial error structure and a logit link function) with occupancy status (1/0) as the response variable and the periphery index as the continuous explanatory variable.

Results

Territory Occupancy and Population Size

We identified a total of 190 potential breeding territories in southern Africa through ground and aerial surveys, and from published sources (Appendix 2.2a). These were territories which were known to be used by Bearded Vultures at some point in the past 52 years. Since all potential breeding cliffs throughout the distribution range were searched during the census period, this was considered the total number of potential territories in southern Africa. Lesotho had 92 territories and South Africa had 98 (Table 2.1).

The total number of breeding territories occupied during the 2000-2012 census period was 109, of which 55 were in Lesotho and 54 were in South Africa (Table 2.1). Of these 109

territories, the percentage of occupancy varied annually between 31% and 75% with an average of 55% of the territories being occupied annually overall (Figure 2.2). Breeding territories were fairly evenly distributed throughout the central and eastern highlands of Lesotho and along the Drakensberg escarpment in KwaZulu-Natal and the Eastern Cape (Figure 2.3). Territories off the main escarpment were located on cliffs along river courses, outlying mountain peaks and sandstone and basalt rock formations above 1,800 m. The remaining 81 territories were classified as either unoccupied (n=12) or abandoned (n=69) by 2012 (Appendix 2.3).

Table 2.1 A comparison of former and current breeding territory occupancy of the Bearded Vulture in southern Africa (known number of sites in each period).

	Former (1960-1999) breeding territory occupancy	Current (2000-2012) breeding territory occupancy
Lesotho	92 (35)	55 (55)
South Africa	98 (80)	54 (54)
Totals	190 (115)	109 (109)

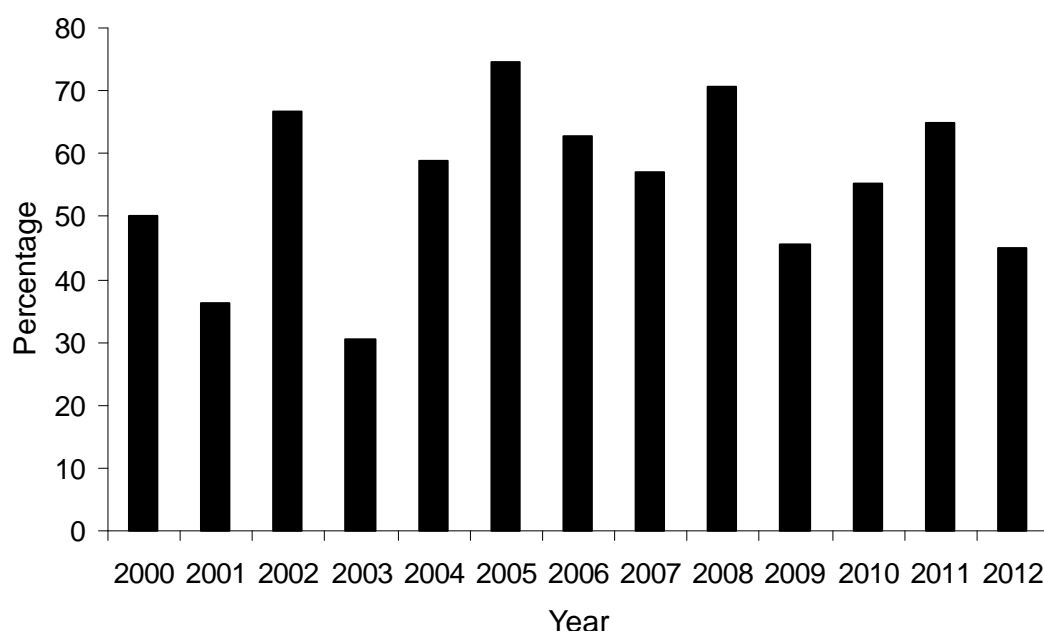


Figure 2.2 Bearded Vulture territory occupancy in southern Africa between 2000 and 2012 where the annual number of occupied territories is depicted as a percentage of the total number of territories occupied between 2000 and 2012 (n=109) that were surveyed.

Of the total number of potential breeding territories ($n=190$), 115 were reported to be occupied during 1960-1999 (Appendix 2.2b, Table 2.1). The status of the remaining 75 during this time is unknown, because these territories were only located during the current census period as a result of increased survey effort. The minimum population decline was explored using a scenario which included only the territories known to be active in the past ($n=115$). A resurvey of these *known* former territories classified 59 territories as abandoned, suggesting a 51% decline (Table 2.2). However, if we allow for the possibility that some apparently abandoned former territories are actually still occupied, with nest sites relocated to new cliffs <7.2 km from the former nest cliffs ($n=22$), then the more conservative overall decline is estimated at 32% (Table 2.2). If we also allow for the unlikely possibility that sites only recorded in 2000-2012 ($n=75$) were newly formed territories not occupied formerly, then the decline is estimated at only 5%.

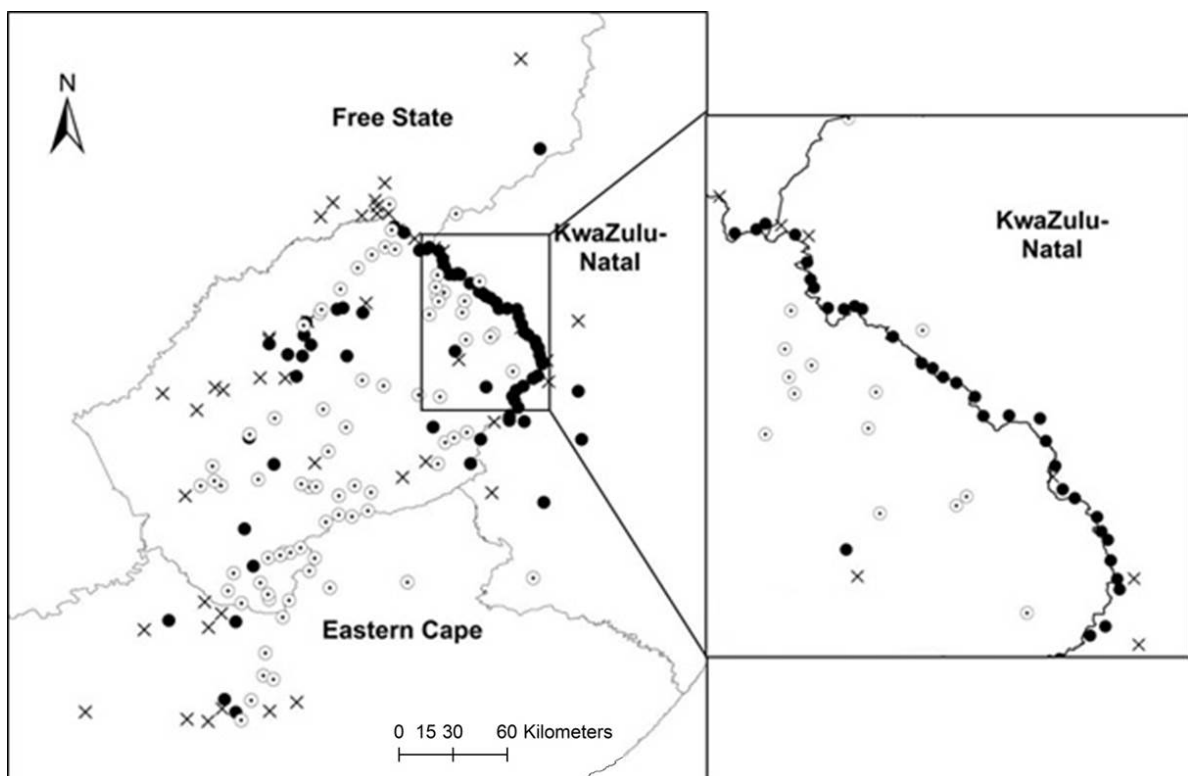


Figure 2.3 A comparison between territories currently (2000-2012) and formerly (1960-1999) occupied (●); territories only located during the current period (2000-2012) but likely to be occupied in the past (⊙); and abandoned territories (X), *i.e.* those only occupied formerly.

Table 2.2 A comparison of the percentage decrease in the number of occupied territories from the number of known and potentially occupied Bearded Vulture territories recorded in southern Africa during the former (1960-1999) and current (2000-2012) period.

Scenario	n	Percentage decrease
1: known number of 115 territories recorded 1960-1999		
a) Minimum number of formerly know territories occupied currently	56	-51%
b) Maximum number of formerly know territories occupied currently	78	-32%
c) Number of currently occupied territories including new ones	109	-5%
2: potential number of 190 territories recorded 2000-2012		
a) Minimum number of potential territories occupied currently	109	-43%
b) Maximum number of potential territories occupied currently	121	-36%

In the second scenario where all potential territories were assumed to be formerly active ($n=190$), the maximum population decline is estimated at 43% ($n=81$) with just over half (57%, $n=109$) the territories currently occupied (Table 2.2). Lesotho and South Africa experienced similar ($\chi^2=0.43$, $df=1$, $P=0.51$) maximum declines of 40% and 45% respectively (Appendix 2.4). There were 12 territories classified as unoccupied but which were only checked between one and three times during this period, primarily through aerial surveys (Appendix 2.5). It is therefore possible that we may have missed the presence of an adult and the territory may have been occupied at some point during this period. Therefore, if we make the conservative assumption that all these territories were actually occupied at some stage during the 2000-2012 period, then the current population comprises a maximum of 121 occupied territories, and would give an estimated minimum population decline of 36% (Table 2.2).

If the 5% decline in known territories is discounted as being unlikely, the maximum decline in the *known* number of territories (51%) is higher than the maximum decline in *potential* territories (43%). The minimum decline in *known* territories (32%) is slightly lower than the minimum decline in *potential* territories (36%), and is probably a more accurate reflection of the actual trend in breeding territory numbers. Either way these different approaches yielded very

similar results and suggest that the decline is real and lies between 32% and 51%. The rate of decline therefore over the past 50 years is between 0.64-1.02% per annum.

All further analyses exploring change were based on the current (minimum) estimate of 109 known occupied territories and the assumption that newly found territories were previously occupied, giving a total of 190 formerly occupied territories.

Current Population Estimate

Based on the current territory occupancy figures ($n=109$ minimum and $n=121$ maximum), the known number of trios in the population ($n=3$), and the age structure of the population (from Chapter 6; 1 adult : 0.67 non-adults), we estimate the southern African Bearded Vulture population to comprise a minimum of 221 breeding adults and 147 non-adult birds and a maximum of 245 breeding adults and 163 non-adult birds. The total current population estimate, therefore, is between 368 and 408 individuals.

Breeding Distribution and Density

The extent of the current breeding range (33,883 km²), as calculated by Minimum Convex Polygon, is 37% less than that of the former breeding range (53,817 km²) and depicts the total study area (Figure 2.4).

The area currently occupied by breeding Bearded Vultures in southern Africa, based on the number of QDSs with territories occupied during the survey period ($n=109$), is 28,125 km², with breeding recorded in 45 QDSs (Figure 2.4). In contrast, the area occupied by the former breeding population, based on all territories known or assumed to have been occupied at least once during 1960-1999 and 2000-2012 ($n=190$), was 38,750 km², with breeding recorded formerly in 62 QDSs (Figure 2.4). This estimate is slightly larger than an earlier estimate of 35,000 km² (Brown 1992) because it incorporates additional QDSs with newly confirmed

breeding territories. If we assume these newly found sites were occupied previously, then the area of occupancy, decreased by 27% over the past five decades. This decrease was greater in South Africa (31%) than in Lesotho (19%) (Table 2.3).

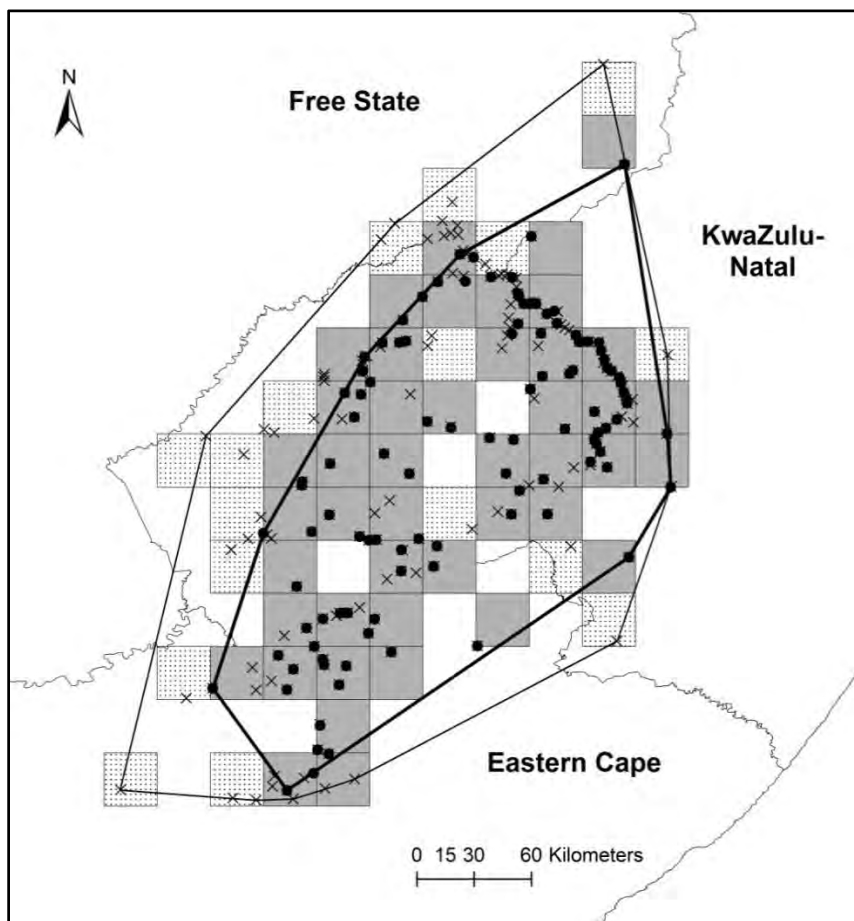


Figure 2.4 A comparison between the current (solid filled: 2000-2012) and former (hashed filled: 1960-1999) breeding distribution of the Bearded Vulture in southern Africa, mapped per Quarter Degree Square (625 km²), within the former (thin line) and current (bold line) extent of the breeding range, showing formerly (x) and currently (•) occupied territories.

Table 2.3 A comparison of the former and current breeding area of occupancy of the Bearded Vulture in southern Africa (where area = number of occupied quarter degree squares multiplied by the area of a quarter degree square).

	Former (1960-1999) area of occupancy	Current (2000-2012) area of occupancy	Percentage decline in area of occupancy
Lesotho	23,125 km ²	18,750 km ²	-19%
South Africa	21,875 km ²	15,000 km ²	-31%
Southern Africa	38,750 km²	28,125 km²	-27%

Consistent with the observed changes in territory occupancy and breeding range, current Bearded Vulture densities of 3.9 occupied territories/1000 km², are 20% lower than the 4.9 occupied territories/1000 km² recorded formerly, *i.e.* based on the assumption that all currently known sites were previously occupied. Consequently, the average inter-nest distance of currently occupied territories is higher (9.0 ± 0.8 km, $n=109$; range 1.3-55.5 km) than the average inter-nest distance of formerly occupied territories (7.7 ± 0.6 km, $n=190$; range 1.0-52.9 km), although this difference is not significant ($F_{1,19}=1.08$, $P=0.32$). The difference in inter-nest distances between the two periods is small because former peripheral territories with greater inter-nest distances were abandoned, resulting in the remaining territories having lower inter-nest distances than expected.

The encounter rate of Bearded Vultures during vehicle survey was 3.14 birds/10 hours in 2012 compared with 6.99/birds/10 hours in 1981, less than half (45%) the number of sightings than in the past. In 2012 a total of 2231 km were driven over a period of 89.4 hours, compared with 1779 km in 100 hours in 1981 (C. Brown *pers. comm.*). Adults were sighted more frequently in 2012 than non-adults in the core areas of the range (Lesotho), whereas non-adults were more commonly sighted in the peripheral areas (Eastern Cape) (Table 2.4). However, the number of adults sighted overall was approximately half the number (51%) sighted in 1981. If all individuals were aged during the survey, the encounter rate of adults may be higher than shown, however the proportion of individuals not aged was higher in 2012 than during 1981.

Table 2.4 The number of individuals sighted per 10 hours along vehicle survey routes during 2012 in the Bearded Vulture's range in southern Africa. The number of individuals sighted in 1981 (C. Brown *pers. comm.*) is given in parentheses for comparative purposes.

Survey Type	Total/ 10 hours	Adults/ 0 hours	Non-adults/ 10 hours	Unknown/ 10 hours
Western Lesotho (core) July 2012	1.89 (7.33)	1.89 (4.33)	0.00 (2.70)	0.00 (0.33)
Eastern Lesotho (core) September 2012	5.95 (9.94)	3.35 (4.14)	2.23 (4.97)	0.37 (0.83)
North-eastern Cape (peripheral) December 2012	1.57 (3.70)	0.00 (1.74)	0.39 (1.96)	1.18 (0.00)
Overall average	3.14 (6.99)	1.75 (3.40)	0.87 (3.21)	0.52 (0.39)

Core versus Peripheral Territories

Visual inspection of the data suggested that more peripheral sites had become abandoned rather than those in the core of the range (Figure 2.5). Of all known territories (n=190), 161 were classified as Core and 29 were classified as Peripheral territories (Figure 2.5). Overall 39% (n=35) and 38% (n=27) of the Core territories in Lesotho and South Africa respectively were abandoned, whereas 100% (n=2) and 63% (n=17) of Peripheral territories in Lesotho and South Africa were abandoned (Figure 2.5).

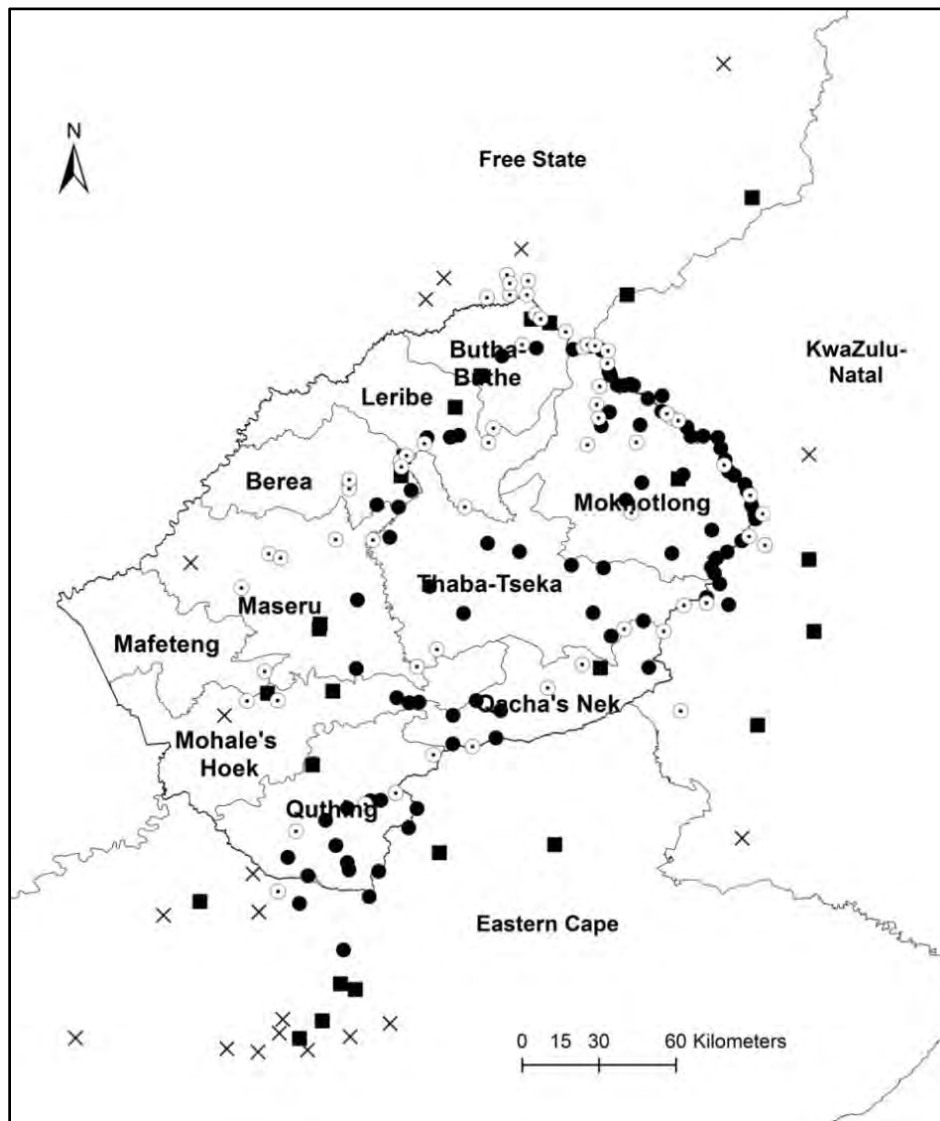


Figure 2.5 The location of currently (2000-2012) occupied Core (●) and Peripheral (■) breeding territories, and abandoned Core (○) and Peripheral (x) territories in the breeding range of the Bearded Vulture in southern Africa.

The location of a territory (in terms of a site's periphery index) had a significant influence on the probability of abandonment ($\chi^2=9.33$, $df=189$, $P=0.002$). Territories that were more peripheral, had a higher probability of abandonment, or put another way, abandoned territories had a lower periphery index (*i.e.* surrounded by less occupied QDS) than occupied territories (abandoned: 5.4 ± 0.2 ; occupied: 6.2 ± 0.1) (Figure 2.6). The current breeding density in the core of the range (4.6 territories/ 1000 km^2) is more than double the density in the periphery of the range (2 territories/ 1000 km^2). Unsurprisingly, Core breeding territories are significantly ($F_{1,109}=0.08$, $P<0.0001$) closer together ($6.7 \pm 0.4 \text{ km}$, $n=84$; range $1.3\text{-}16.4 \text{ km}$) than Peripheral territories ($16.4 \pm 2.7 \text{ km}$, $n=25$; range $1.7\text{-}55.5 \text{ km}$).

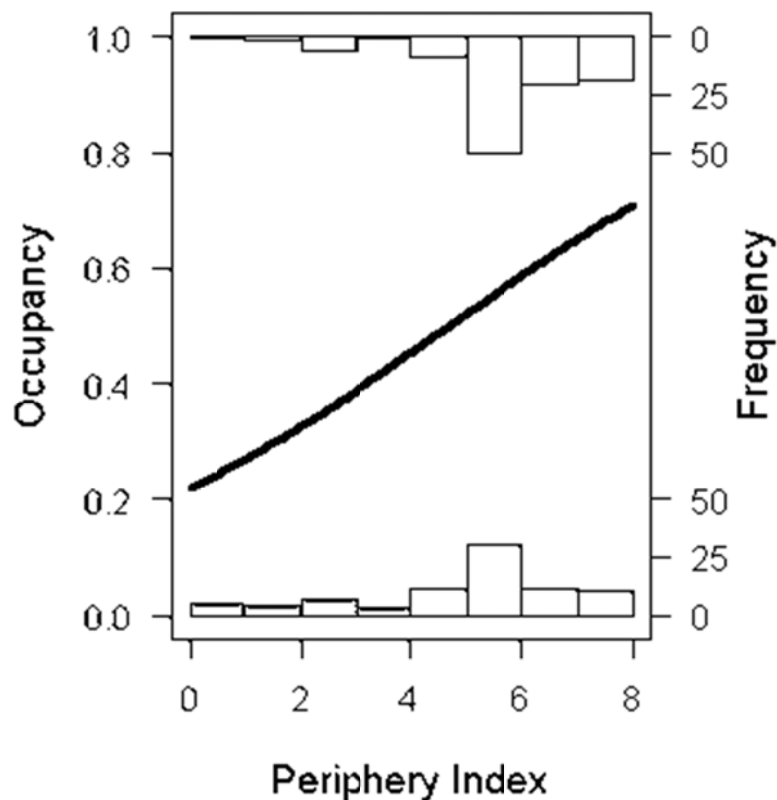


Figure 2.6 The relationship between probability of territory occupancy (where '0' is abandoned and '1' is occupied) and region. The line is the fitted line from a Binomial Generalized Linear Model. The probability of occupancy increases with an increase in the periphery index (where '0' is Peripheral and '8' is Core), which is based on the number of surrounding Quarter Degree Squares which contained breeding Bearded Vultures.

Discussion

This study confirmed the decrease of the Bearded Vulture in southern Africa documented by Krüger *et al.* (2006). This study quantified decreases in territory occupancy (by 32-51%), breeding distribution (by about 27%) and density (by about 20%) over the last 52 years, and verified that territory abandonment has been more frequent around the periphery of the species' range. The rate of population decline was between 0.64-1.02 per annum. In addition, there was a 45% reduction in the encounter rate of individuals within the range over a 30 year period. Our results suggest that recommendations to address the already severe declines documented in the 1980s (Brown 1991) have either not been implemented or have not been sufficient to adequately arrest these negative trends.

The recent extensive and thorough census revealed a slightly larger former breeding range, with new breeding territories that were not previously recorded by Brown (1992). Our estimates of former breeding range (38,750 km²), breeding density (3.9 pairs/1000 km²) and breeding population (190 pairs), are very similar to the estimates of 35,000 km², 3.4-7.2 pairs/1000 km² and 204 pairs respectively derived by Brown (1992), despite only 30% of the territories being known at that time. Our estimate of the current number of breeding territories in Lesotho (55) is at the lower end of a more recent, independent estimate of 55-70 breeding territories (Kopij 2004).

Although there has been a reduction in breeding density, the density recorded during this study (3.9 pairs/1000 km²) is within the range of densities recorded for various regions within the Spanish Pyrenees (0.14-7.4 pairs/1000 km²), with the highest densities being recorded in the core region (Margalida *et al.* 2003, Carrete *et al.* 2006, Margalida *et al.* 2007, Gómez de Segura *et al.* 2012). Similarly the average nearest neighbour distance in our population (9.0 km) was within the range of 2.1-28.0 km and 8.9-11.1 km recorded in the Spanish Pyrenees (Donazar *et al.* 1993, Margalida *et al.* 2008b). Although the results allow for interesting comparisons with wild populations elsewhere, the densities recorded in the Spanish Pyrenees are those of a recovering population with an important network of supplementary

feeding sites which probably promotes territory shrinkage (Margalida *et al.* 2008b) and therefore may not be a real reflection of natural densities.

Breeding densities were highest in the core of the range along the Maloti-Drakensberg escarpment and in the Lesotho Highlands but many breeding territories off the main escarpment in South Africa have been abandoned. Our study therefore, confirms the previously documented abandonment of territories in the lowlands (Maphisa 1997) and peripheral areas of the range (Colahan and Esterhuizen 1997). The population has exhibited a contraction in breeding range as well as a contraction to the centre of the breeding range, evidenced by the greater chance of abandonment in the peripheral areas and higher territory densities in the core areas than in the peripheral areas. This observed decline supports the patterns identified by Mayfield (1972, 1973a, 1973b) and Wilcove and Terborgh (1984) who recorded reduced densities in marginal and sub-optimal habitats and contraction toward the centre of the species' range as populations decline. Our findings also show some support for the “melting range” analogy (Rodríguez 2002); as a population declines in abundance, it becomes increasingly rare in peripheral areas and experiences a range reduction, and remaining territories occupy the range where densities were higher before the decline. Knowledge of the mechanisms of decline and the underlying local densities is required to interpret the patterns in range contraction and density reduction for the monitoring and conservation of the species to be more effective (Schonewald-Cox and Buechner 1991). These mechanisms, such as food availability, climatic factors or human density and associated infrastructure require further investigation.

The declines shown, and the potential threats discussed, in this study are reflected by a number of studies on other sub-populations of Bearded Vulture (e.g. Frey 1996, Mingozi and Estève 1997, Del Hoyo *et al.* 1994, Carrete *et al.* 2006, Margalida *et al.* 2008a) and on other vulture populations in Africa (Rondeau and Thiollay 2004, Thiollay 2007, Virani *et al.* 2011, Ogada *et al.* 2012). Regionally, cliff-nesting Cape Vultures *Gyps coprotheres* have also declined in range and numbers throughout the Maloti-Drakensberg mountains and adjacent areas (Piper

1997, Vernon and Boshoff 1997, Anderson 2000b, Allan and Jenkins 2006, Boshoff *et al.* 2009), possibly as a result of a similar suite of driving forces.

Tall cliffs are ubiquitous throughout the Lesotho highlands and along the Drakensberg escarpment, and this together with the fact that there were many unoccupied territories, provides further support for Brown *et al.*'s (1988) previous conclusion that the availability of suitable breeding territories is not a limiting factor in the size of the southern African breeding Bearded Vulture population. The original range contraction and population decline that restricted the species to its current range were attributed to persecution by humans (shooting, poisoning and disturbance at nests) and a decrease in the availability of carrion (Siegfried *et al.* 1976), although studies in Spain have shown that food shortages affect this species to a lesser degree (Margalida and Colomer 2012). More recently, decreasing numbers have been attributed to poisoning (Brown 1991), displacement by humans and livestock at lower altitudes and degradation of habitat (Mundy *et al.* 1992, Vernon and Boshoff 1997), and the deliberate persecution of vultures for traditional medicine, food and ceremonial purposes (Maphisa 1997, Ngwenya 2001, Mander *et al.* 2007). We also cannot exclude the possibility that climatic factors have forced birds into higher and cooler sites and reduced the breeding population over this time period (Simmons and Jenkins 2007) as predicted for other southern African birds (Simmons *et al.* 2004).

The past few decades have seen a large increase in the size of the human population and associated developments within the region (Statistics South Africa 2011). We hypothesize that anthropogenic influences are driving the abandonment of Bearded Vulture territories, particularly on the periphery of the breeding range, but the exact mechanics of this interaction remain unknown and will be investigated further in Chapter 3. Non-natural mortalities attributed to illegal poisoning have been the main mortality factor in other populations (Margalida 2012). In Chapter 6, we examine whether poisoning, either direct (for traditional medicine purposes) and/or indirect (through ingesting carcasses containing harmful veterinary drugs or poisoned bait for predator control), is also still a major mortality factor for the population in southern

Africa. Information on nesting success and survival of different age classes will also be investigated in Chapter 6 to determine whether either may be a contributing factor to the species' decline documented in this chapter.

Our findings have ensured a more accurate reassessment of the species' conservation status and served to substantiate the regional uplisting of the species to Critically Endangered (Krüger *in press*). We show patterns of decline consistent with other studies that have documented the collapse of several vulture populations throughout Africa in the past decade (Rondeau and Thiollay 2004, Thiollay 2007, Virani *et al.* 2011, Ogada *et al.* 2012). Collectively, these results are suggestive of an "African Vulture Crisis", and motivate for an urgent, informed and concerted conservation effort to ensure the continued survival of vultures across the African continent. A number of conservation measures, such as supplementary feeding, have been successfully implemented elsewhere to address food shortages, the effects of direct and indirect poisoning and to improve breeding success (Piper *et al.* 1999, Margalida *et al.* 2003, Oro *et al.* 2008). These measures must be investigated for the potential effectiveness of their implementation for this population.

Acknowledgements

We are grateful to Ezemvelo KwaZulu-Natal Wildlife, the Wildlands Conservation Trust, the Maloti Drakensberg Transfrontier Programme, Sasol through the Endangered Wildlife Trust, Free State Economic Development, Tourism and Environmental Affairs, the South African Air Force and the Durban National Science Museum for their generous funding and assistance with the various surveys during the census period. We thank the many dedicated volunteers and individuals from various organisations who assisted with the surveys, in particular Ezemvelo KwaZulu-Natal Wildlife staff (Douglas van Zyl, Peter Chadwick, Alan Howell, John Crowson, Eduard Goosen and the Ecological Advice Staff, Field Rangers and Conservation Managers throughout the Maloti Drakensberg Park World Heritage Site) and Richard Lechmere-Oertel.

The following individuals are thanked for making their unpublished information available: David Ambrose, Robin Guy, Wigbert Vogeley, Brian Colahan and especially Christopher Brown. Rob Simmons is thanked for commenting on an earlier draft of this manuscript.

References

- Acharya R, Cuthbert R, Baral HS and Chaudhary A (2010) Rapid decline of the Bearded Vulture *Gypaetus barbatus* in Upper Mustang, Nepal. *Forktail* 26: 117-120.
- Allan DG and Jenkins AR (2006) Status Report and Monitoring Plan for the Bearded and Cape Vultures in Lesotho. Part 1: Status of breeding sites of Bearded and Cape Vultures in Lesotho based on a review and field surveys. Maloti Drakensberg Ecology Consultants cc. *unpubl report*.
- Anderson MD (2000a) Bearded Vulture *Gypaetus barbatus*. In: Barnes KN (editor) The Eskom Red Data book of birds of South Africa, Lesotho and Swaziland. BirdLife South Africa, Johannesburg, pp. 39-41.
- Anderson MD (2000b) Cape Vulture *Gyps coprotheres* P In: Barnes KN (editor) The Eskom Red Data book of birds of South Africa, Lesotho and Swaziland. BirdLife South Africa, Johannesburg, pp. 39-41.
- Ash J and Atkins J (2009) Birds of Ethiopia and Eritrea: an atlas of distribution. Christopher Helm, London.
- Beyer HL (2004) Hawth's analysis tools for ArcGIS. Available at <http://www.spataleecology.com/htools>.
- BirdLife International (2014) IUCN Red List for birds. Downloaded from <http://www.birdlife.org> on 05/08/2014.
- Boshoff AF, Brooke RK and Crowe TM (1978) Computerized distribution mapping scheme for vertebrates in southern Africa. *S Afr J Wildl Res* 8: 145-149.

- Boshoff AF, Vernon CJ and Brooke RK (1983) Historical atlas of the diurnal raptors of the Cape Province (Aves: Falconiformes). *Ann Cape Prov Mus (Nat Hist Ser)* 14: 173-297.
- Boshoff A, Piper S and Michael M (2009) On the distribution and breeding status of the Cape Griffon *Gyps coprotheres* in the Eastern Cape province, South Africa. *Ostrich* 80: 85–92.
- Brooke RK (1984) South African Red Data Book- Birds. *S Afr Nat Sci Prog Rep* 97. CSIR, Pretoria.
- Brown CJ (1990) Breeding biology of the Bearded Vulture in southern Africa, Parts I – III. *Ostrich* 61: 24-49.
- Brown CJ (1991) An Investigation into the decline of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Biol Conserv* 57: 315-337.
- Brown CJ (1992) Distribution and status of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Ostrich*. 63: 1-9.
- Brown CJ (1997) Population dynamics of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Afr J Ecol* 35: 53-63.
- Brown CJ, Brown SE and Guy JJ (1988) Some physical parameters of Bearded Vulture *Gypaetus barbatus* nest sites in southern Africa. Proceedings of the VI Pan-African Ornithological Congress, pp. 139-152.
- Carrete M, Donázar JA and Margalida A (2006) Density dependent productivity depression in Pyrenean Bearded Vultures: Implications for conservation. *Ecol Appl* 16: 1674–1682.
- Colahan BD and Esterhuizen JR (1997) The status and conservation of vultures in the Free State Province, South Africa. In: Boshoff AF *et al.* (editors) Vultures in the 21st Century. Proceedings of a Workshop on Vulture Research and Conservation in Southern Africa. Vulture Study Group, Johannesburg, pp. 46-49.

- Del Hoyo J, Elliott A and Sargatal J (1994) Handbook of the Birds of the World. Vol 2. Lynx Edicions, Barcelona.
- Donazar JA, Hiraldo F and Bustamante J (1993) Factors Influencing Nest Site Selection, Breeding Density and Breeding Success in the Bearded Vulture (*Gypaetus barbatus*). *J Appl Ecol* 30: 504-514.
- Frey H (1996) The situation of the Bearded Vulture (*Gypaetus barbatus*) in the Mediterranean countries. In: Muntaner J and Majol J (editors) *Biología y Conservación de las Rapaces Mediterráneas*, 1994. Monografías 4, SEO, Madrid.
- Godino A, Paz JL, Mouati N and Simón MA (2005) Three Years of Bearded Vultures' Surveys in Morocco. In: Frey H, Schaden G and Bijleveld van Lexmond M (editors) *Bearded Vulture Annual Report 2005*. Foundation for the Conservation of the Bearded Vulture (FCBV), Wassenaar, The Netherlands.
- Gómez de Segura AG, Martínez JM and de la Fuente MA (2012) Population size of the endangered vulture *Gypaetus barbatus* in Aragon (Spain): an approximation to the Pyrenean population. *Ardeola* 59: 43-55.
- Hiltunen TA (2008) *Farmers and the Bearded Vulture Gypaetus barbatus meridionalis*. Dissertation, University of Pretoria.
- Hiraldo F, Delibes M and Calderon J (1979) *El Quebrantahuesos: sistemática, taxonomía, biología, distribución y protección*. Monografías 22, ICONA, Madrid.
- Kopij G (2004) Status and conservation of the Bearded Vulture *Gypaetus barbatus meridionalis* in Lesotho. In: Frey H, Schaden G and Bijleveld van Lexmond M (editors) *Bearded Vulture Annual Report 2004*. Foundation for the Conservation of the Bearded Vulture (FCBV), Wassenaar, The Netherlands.

- Krüger S (*in press*) Bearded Vulture. In: Taylor MR (editor) The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. BirdLife South Africa, Johannesburg.
- Krüger S, Piper S, Rushworth I, Botha A, Daly B, Allan D, Jenkins A, Burden D and Friedmann Y (editors) (2006) Bearded Vulture (*Gypaetus barbatus meridionalis*) Population and Habitat Viability Assessment Workshop Report. Conservation Breeding Specialist Group (SSC/IUCN)/CBSG Southern Africa. Endangered Wildlife Trust, Johannesburg.
- Mander M, Diederichs N, Ntuli L, Khulile M, Williams V and McKean S (2007) Survey of the Trade in Vultures for the Traditional Health Industry in South Africa. Futureworks, *unpubl report*, 30pp.
- Maphisa DH (1997) Vultures in Lesotho: past, present and future. In: Boshoff AF *et al.* (editors) Vultures in the 21st Century. Proceedings of a Workshop on Vulture Research and Conservation in Southern Africa. Vulture Study Group, Johannesburg, pp. 93-96.
- Margalida, A (2012) Baits, budget cuts: a deadly mix. *Science* 338: 192.
- Margalida A, García D, Bertran J and Heredia R (2003) Breeding biology and Success of the Bearded Vulture *Gypaetus barbatus* in eastern Pyrenees. *Ibis* 145: 244-252.
- Margalida A, García D and Cortés-Avizanda A (2007) Factors influencing the breeding density of Bearded Vultures, Egyptian Vultures and Eurasian Griffon Vultures in Catalonia (NE Spain): management implications. *Anim Biodiv Conserv* 30(2): 189-200.
- Margalida A, Heredia R, Razin M and Hernandez M (2008a) Sources of variation in mortality of the Bearded Vulture *Gypaetus barbatus* in Europe. *Bird Conserv Int* 18: 1-10.
- Margalida A, Donazar JA, Bustamante J, Hernández FJ and Romero-Pujante M (2008b) Application of a predictive model to detect long-term changes in nest-site selection in the Bearded Vulture *Gypaetus barbatus*: conservation in relation to territory shrinkage. *Ibis* 150: 242-249.

- Margalida A, Oro D, Cortés-Avizanda A, Heredia R and Donázar JA (2011) Misleading population estimates: biases and consistency of visual surveys and matrix modelling in the endangered Bearded Vulture. *PLoS ONE* 6: e26784.
- Margalida A and Colomer MA (2012) Modelling the effects of sanitary policies on European vulture conservation. *Sci Rep* 2: 753.
- Mayfield HF (1972) Third decennial census of Kirtland's Warbler. *Auk* 89: 263-268.
- Mayfield HF (1973a) Census of Kirtland's Warbler in 1972. *Auk* 90: 684-685.
- Mayfield HF (1973b) Kirtland's Warbler Census, 1973. *Am Birds* 27: 950-952.
- Mingozzi T and Estève R (1997) Analysis of a historical extirpation of the Bearded vulture *Gypaetus barbatus* (L.) in the Western Alps (France-Italy): former distribution and causes of extirpation. *Biol Conserv* 79: 155-171.
- Mundy P, Butchart D, Ledger J and Piper S (1992) The Vultures of Africa. Russel Friedman Books cc, Johannesburg, South Africa.
- Ngwenya NP (2001) Implications of the medicinal animal trade for Nature Conservation in KwaZulu-Natal. Ezemvelo KZN Wildlife *unpubl report*, 76pp.
- Ogada DL, Keesing F and Virani MZ (2012) Dropping dead. Causes and consequences of vulture population declines worldwide. *Ann NY Acad Sci* 1249: 57-71.
- Oro D, Margalida A, Carrete M, Heredia R, Donázar JA (2008) Testing the Goodness of Supplementary Feeding to Enhance Population Viability in an Endangered Vulture. *PLoS ONE* 3: e4084.
- Piper SE (1997) The status and distribution of vultures in the KwaZulu-Natal Province, South Africa. In: Boshoff AF *et al.* (editors) *Vultures in the 21st Century*. Proceedings of a Workshop on Vulture Research and Conservation in Southern Africa. Vulture Study Group, Johannesburg, pp. 93-96.

- Piper SE, Boshoff AF and Scott HA (1999) Modelling survival rates in the Cape Griffon *Gyps Coprotheres*, with emphasis on the effects of supplementary feeding. *Bird Study* 46: 230-238.
- Rodríguez JP (2002) Range contraction in declining North American bird populations. *Ecol Appl* 12: 238-248.
- Rondeau G. and Thiollay JM (2004) West African vulture decline. *Vulture News* 51: 13-33.
- Schonewald-Cox C and Buechner M (1991) Housing viable populations in protected habitats: the value of coarse-grained geographic analysis of density patterns and available habitat. In: Seitz A and Loeschcke V (editors) *Species conservation: a population-biological approach*. Birkhauser, Basel, Switzerland.
- Shimelis A (2011) The Status of Raptors in Ethiopia. Downloaded from <http://www.africanraptors.org/the-status-of-raptors-in-ethiopia-by-anteneh-shimelis> on 13/05/2012.
- Siegfried WR, Frost PGH, Cooper J and Kemp AC (1976) Rare and vulnerable birds in South Africa. *Biol Conserv* 10: 83-93.
- Simmons RE, Barnard P, Dean WRJ, Midgley GF, Thuiller W and Hughes G (2004) Climate change and birds: perspectives and prospect from southern Africa. *Ostrich* 75: 295-308.
- Simmons RE and Jenkins AR (2007) Is climatic change influencing the decline of Cape and Bearded Vultures in southern Africa? *Vulture News* 56: 41-51.
- Statistics South Africa (2011) Mid-year population estimates 2011. Statistical release, P0302, Pretoria, South Africa.
- Terrasse JF (2001) *Le gypaète barbu*. Delachaux et Niestlé, Lusanne, Switzerland.
- Thiollay JM (2007) Raptor population decline in West Africa. *Ostrich* 78: 405–413.

- Vernon CJ and Boshoff AF (1997) A review of the status of vultures in the Eastern Cape Province, South Africa. In: Boshoff AF *et al.* (editors) Vultures in the 21st Century. Proceedings of a Workshop on Vulture Research and Conservation in Southern Africa. Vulture Study Group, Johannesburg, pp. 50-56.
- Virani MZ, Kendall C, Njoroge P and Thomsett S (2011) Major declines in the abundance of vultures and other scavenging raptors in and around the Masai Mara ecosystem, Kenya. *Biol Conserv* 144: 746-752.
- Whitfield DP, Fielding AH, McLeod DRA, Haworth PF and Watson J (2006) A conservation framework for the golden eagle in Scotland: Refining condition targets and assessment of constraint influences. *Biol Conserv* 130: 465–480.
- Wilcove DS and Terborgh JW (1984) Patterns of population decline in birds. *Am Birds* 38: 10-13.
- Xirouchakis S, Sakoulis A and Andreou G (2001) The decline of the Bearded Vulture *Gypaetus barbatus* in Greece. *Ardeola* 48(2): 183-190.
- Zimmerman DA, Turner DA and Pearson DJ (1996) Birds of Kenya and northern Tanzania. Princeton University Press, Princeton, New Jersey.

Appendices

Appendix 2.1 Published records and unpublished reports from which the location of former breeding territories was obtained.

Allan DG (1996) Report on survey of birds downstream of Mohale Dam on the Senqunyane and Senqu rivers. *ADU Res Rep* 19: 1-71.

Allan DG (2001) The impact of the inundation of Katse Dam in the Lesotho highlands on the local avifauna, based on a comparison of information collected during a pre-inundation baseline survey (1991) and a post-inundation monitoring study (1996-2000) - LHDA Project 615 - Birds. Durban Natural Science Museum Bird Department Research Report 13: 1-351.

Allan DG, Barnes KN, Jenkins AR and Whittington P (1996) Baseline Biological Survey, Fauna and Flora, Lesotho Highlands Water Project Phase 1B Mohale Dam - Birds. *ADU Res Rep* 18: 1-126.

Ambrose D (2005) Lesotho annotated bibliography. Section 167. Birds including annotated species checklist. Second edition. House 9 Publications, Roma University of Lesotho, Roma, Lesotho.

Ambrose D and Maphisa DH (1999) Guide to the birds of the Roma Campus, National University of Lesotho. National University of Lesotho Publishing House, Roma, Lesotho.

British Schools Exploration Society (BSES) (2003) Lesotho 2003 – Ornithological File. BSES *unpubl report*.

Brown CJ (1990) Breeding biology of the Bearded Vulture in southern Africa, Parts I – III. *Ostrich* 61: 24 - 49.

Brown CJ (1991) An Investigation into the decline of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Biol Conserv* 57: 315-337.

Jacot-Guillarmod C (1963) Catalogue of the birds of Basutoland. *S Afr Avi Ser* 8: 1-111.

Kopij G (2002) The birds of Sehlabathebe National Park. *Koedoe* 45: 65-78.

Kopij G (2004) Status and conservation of the Bearded Vulture *Gypaetus barbatus meridionalis* in Lesotho. In: Frey H, Schaden G and Bijleveld van Lexmond M (editors) Bearded Vulture Annual Report 2004. Foundation for the Conservation of the Bearded Vulture (FCBV), Wassenaar, The Netherlands.

Maphisa DH (1997) Vultures in Lesotho: past, present and future. In: Boshoff AF *et al.* (editors) Vultures in the 21st Century. Proceedings of a Workshop on Vulture Research and Conservation in Southern Africa, Vulture Study Group, Johannesburg, pp. 93-96.

Maphisa DH (2001) British Schools Exploration Society's (BSES) survey of vultures at selected sites in Lesotho – July to August 1998. *Vulture News* 45: 11-19.

Osborne PE and Tigar BJ (1990) The status and distribution of birds in Lesotho, *unpubl report*.

van Zyl D (2001) Vulture Survey- uKhahlamba Drakensberg Park 2001. Ezemvelo KZN Wildlife *unpubl report*, 13pp.

van Zyl D (2002) Preliminary results of a Vulture Survey in the uKhahlamba Drakensberg Park - July 2002. Ezemvelo KZN Wildlife *unpubl report*, 9pp.

Appendix 2.2a The number of breeding territories depicted by survey frequency and survey type during 2000-2012.

Survey frequency	Survey Type			Totals
	Aerial	Ground	Combination	
Once	25	18	0	43 (23%)
2-3 times	20	10	31	61 (32%)
4-6 times	1	10	19	30 (16%)
7-13 times	0	5	51	56 (29%)
Totals	46 (24.2%)	43 (22.6%)	101 (53.2%)	190

Appendix 2.2b The number of breeding territories depicted by survey frequency and survey type during 1960-1999.

Survey frequency	Survey type				Totals
	Aerial	Ground	Aerial and ground	Other*	
Once	69	10	0	0	79 (69%)
2-6 times	0	17	5	5	27 (23%)
7-13 times	0	1	0	0	1 (0.9%)
Unknown	0	0	0	8	8 (7%)
Totals	69 (60%)	28 (24.3%)	5 (4.3%)	13 (11.3%)	115

* Information obtained from unpublished reports where the survey type was unknown

Appendix 2.3 The number of breeding territories depicted by survey frequency and territory status during 2000-2012.

Survey Frequency	Territory status		
	Occupied	Unoccupied	Abandoned
Once	20	9	14
2-3 times	29	3	29
4-6 times	22	0	8
7-13 times	38	0	18
Totals	109	12	69

Appendix 2.4 A comparison of the former (1960-1999) and current (2000-2012) breeding territory occupancy of the Bearded Vulture in southern Africa, depicted by district in Lesotho and by province in South Africa.

Region	Former breeding territory occupancy	Current breeding territory occupancy	Percent loss
Lesotho: Butha Buthe	5	4	20
Lesotho: Leribe	8	4	50
Lesotho: Berea	11	5	55
Lesotho: Mokhotlong	16	10	38
Lesotho: Mophale's Hoek	9	6	33
Lesotho Maseru	9	4	56
Lesotho: Mafeteng	1	0	50
Lesotho: Thaba Tseka	12	8	33
Lesotho: Quachas Nek	8	5	38
Lesotho: Quthing	13	9	39
<i>Lesotho sub-total</i>	<i>92</i>	<i>55</i>	<i>40</i>
South Africa: Free State Province	17	3	82
South Africa: KwaZulu-Natal Province	53	35	34
South Africa: Eastern Cape Province	28	16	43
<i>South Africa sub-total</i>	<i>98</i>	<i>54</i>	<i>45</i>
Totals	190	109	43

Appendix 2.5 The number of breeding territories depicted by survey type and territory status during 2000-2012.

Survey type	Territory status		
	Occupied	Unoccupied	Abandoned
Aerial	22	9	15
Ground	29	1	12
Combination	58	2	42
Total	109	12	69

**Chapter 3: Anthropogenic activities influence the abandonment
of Bearded Vulture *Gypaetus barbatus* territories in
southern Africa**



Photo 3 Adult Bearded Vulture foraging amongst anthropogenic activities

A modified form of this chapter has been accepted by The Condor and is currently in press:

Krüger SC, Simmons RE and Amar A (*in press*) Anthropogenic activities influence the abandonment of Bearded Vulture *Gypaetus barbatus* territories in southern Africa.

Abstract

Developing an effective conservation strategy for a critically endangered species relies on identifying the most pressing threats to the species. One approach to elucidate these threats is to examine which factors are associated with territorial abandonment. The Bearded Vulture has declined dramatically in southern Africa over the past few decades, with nearly 50% of known territories being abandoned. In this study we examine the evidence for three hypotheses, that territorial abandonment was associated with (1) human impact, (2) food availability or (3) climate change, or a combination of these. Model selection was used to determine the importance of seven covariates within the home range of an adult pair, an area of 10 km radius (314 km²) around each territory. Our analyses provided strongest support for the human impact hypothesis, with abandonment more likely in territories with more power lines and higher densities of human settlements. Additionally, within Lesotho, there was some support for the food shortage hypothesis, with territories more likely to have remained occupied where they had a greater number of feeding sites within close proximity. Our data provided no support for the hypothesis that climate change may be driving abandonment, with no associations between abandonment and either altitude or aspect of the nest site. Our results are in accordance with the main causes of mortality which were found to be poisoning and power line collisions, and suggest that conservation measures should focus on limiting the development of further human settlements and power lines within 10 km of occupied territories, applying mitigation measures to existing power lines and increasing law enforcement and education in areas still occupied by the species.

Introduction

Unprecedented numbers of animal and plant species face extinction as a result of anthropogenic actions, climate change and/or invasive alien species (De Salle and Amato 2004, Heller and Zavaleta 2009). Anthropogenic actions have been responsible for the loss of habitat

and the decline in individual populations of many species in the past few decades (Butchart *et al.* 2010, Convention on Biological Diversity 2010) and global climate change is predicted to cause species' extinctions and distributional shifts (Midgley *et al.* 2001, Erasmus *et al.* 2002, Thomas *et al.* 2004) as well as range contractions (Huntley and Barnard 2012) in the next few decades.

The scavenger guild is threatened around the globe (Hoffmann *et al.* 2010), and avian scavengers have the highest percentage of extinction-prone species among avian functional groups (Sekercioglu *et al.* 2004). Vultures in particular have experienced large population declines worldwide as a result of loss of suitable breeding and foraging habitat and poisoning (Green *et al.* 2004, Oaks *et al.* 2004, Ogada *et al.* 2012). The Bearded Vulture *Gypaetus barbatus* is also showing declines throughout much of its range (Mingozzi and Estève 1997, Margalida *et al.* 2008, Birdlife International 2014). Within southern Africa, where the breeding population has declined in both numbers (between 32-51%) and range (27%) over the past five decades (Krüger *et al.* 2014, Chapter 2), the species was recently up-listed to Critically Endangered (Krüger *in press*). The southern African population is restricted to the Maloti-Drakensberg mountains of South Africa and Lesotho (Brown 1997, Krüger *et al.* 2014, Chapter 2) where pairs occupy a territory containing one or more nests on high cliffs generally >1,800 m above sea level (Brown 1988, Heredia 1991).

There is an urgent need to identify the factors responsible for the decline of this population. To do this we use Caughley's (1994) declining population paradigm, postulating a series of plausible hypotheses and then testing which factors associated with these hypotheses were most closely linked to the abandonment of breeding territories. Similar approaches have been successful in elucidating important factors constraining other bird populations (e.g. Lewis *et al.* 2007, Buchanan *et al.* 2004, Amar *et al.* 2010). In this study we explore the evidence for the following three *a priori* hypotheses: (1) Territorial abandonment has been caused by anthropogenic activity, with abandonment occurring in areas with greater exposure to human impact. (2) Territorial abandonment is the result of food shortages, with territories being

abandoned in areas with insufficient food. (3) Territorial abandonment is being driven by climate change with abandonment occurring at locations which are being most affected by climate change.

The theoretical basis for hypothesis (1) has considerable support. Global vulture declines and declines in Bearded Vulture populations have largely been attributed to human impacts, namely human persecution for traditional medicine, food, ceremonial and other purposes (Maphisa 1997, Xirouchakis *et al.* 2001, Mander *et al.* 2007, Thiollay 2007), indirect poisoning through poison baiting of carnivores (Brown 1991) and use of veterinary drugs (Green *et al.* 2004, Oaks *et al.* 2004), collisions with power lines (Krüger *et al.* 2006), or a combination of these factors (Margalida *et al.* 2008, Ogada *et al.* 2012). The historical declines of the southern African Bearded Vulture population have also been attributed to anthropogenic factors (Siegfried *et al.* 1976, Brown 1991, Mundy *et al.* 1992) but the mechanisms for the more recent declines are not well understood. The past few decades have seen a large increase in the human population and associated developments, such as energy infrastructure, within the region (Kalipeni 1994, Energy Sector Policy of the AfDB group 2012) which may be driving the abandonment of territories through the continued exposure of the Bearded Vulture population to unnatural mortality factors. To explore this first hypothesis, we examine whether abandonment was associated with three factors: (i) Density of human settlements surrounding territories, as we predict that persecution levels might be highest in areas within relatively close proximity to human settlements. (ii) Abundance of power lines, because of their documented impact on other vulture and large raptor populations through collisions and electrocutions (Lehman *et al.* 2007, Smallie and Virani 2010, Boshoff *et al.* 2011). (iii) The amount of area surrounding a territory that is under formal protection, since we would expect that territories in protected areas would be insulated and shielded to a greater degree from all anthropogenic threats.

The alternative hypothesis (2) for abandonment, decreased food availability, caused by habitat loss and change in land use, has been previously considered as a potential mechanism for the wider historical decline of the species in southern Africa (Siegfried *et al.* 1976, Mundy *et*

al. 1992), although Brown (1991) did not believe it to be an important driving factor for the local declines witnessed more recently. Food availability is known to affect nest site selection and breeding success of Bearded Vulture populations in Europe (Donazar *et al.* 1993, Gavashelishvili and McGrady 2006, Margalida *et al.* 2007). The Bearded Vulture is an obligate scavenger requiring carrion of primarily medium sized ungulates (Hiraldo *et al.* 1979, Brown 1997). Livestock graze throughout the species' foraging range and are scavenged from communal grazing lands in Lesotho or commercial livestock farms in South Africa, whereas wild ungulates are scavenged predominantly from protected areas. Related to our food shortage hypothesis, we also investigate whether the presence of more predictable food resources, in the form of supplementary feeding sites, influences territory occupancy, since many other vulture populations have been found to be heavily reliant on supplementary feeding (Piper 2005, Deygout *et al.* 2009, Cortés-Avizana *et al.* 2010, Phipps *et al.* 2013). We use livestock and ungulate density as a surrogate for the availability of carrion, and predict that if food supply influences territorial occupancy then it will be positively related to the number of ungulates and the presence of supplementary feeding sites in the landscape.

Hypothesis (3) relates to climate change because Bearded Vultures live in cold, high-altitude climates in a continent that is rapidly warming. The Bearded Vulture is considered particularly vulnerable to the impacts of climate change being a long-lived, territorial species, occurring at a low density with low reproductive rates within a restricted distribution range (Simmons *et al.* 2004). Africa is considered the continent most at risk from climate change (Hulme 1996, Kruger and Sekele 2012, IPCC 2014) and Lesotho in particular is showing rapid warming (Mokotjomela *et al.* 2010). Huntley and Barnard (2012) and Huntley *et al.* (2012) have modelled the relationships between species spatial abundance patterns and climate, and predict a range contraction for the Bearded Vulture. Although climate change will occur across a broad landscape scale, not all territories would be equally exposed to any negative effects. Since the species is limited to higher altitudes it is vulnerable because it lacks escape options (Thomas *et al.* 2004), and Colahan and Esterhuizen (1997) and Simmons and Jenkins (2007)

noted that many Bearded and Cape Vulture *Gyps coprotheres* nest sites in the lower altitude regions were abandoned whereas higher altitude sites were still occupied. Nests are built in potholes/small caves or on ledges with overhangs (Hiraldo *et al.* 1979) and nest entrances generally face cooler aspects (e.g. south in southern Africa) which offer the best shelter against sun, wind and precipitation (Brown 1988, Gavashelishivili and McGrady 2006). Nest site altitude and aspect will therefore be considered as surrogates for temperature to investigate climate change which may drive territorial abandonment since nest sites at lower altitudes and those with entrances facing north and east would experience the highest temperatures.

In this chapter we explore the evidence for these three hypotheses by examining which covariates (linked to the different hypotheses) are most closely associated with territorial abandonment. Furthermore, we compare these results with known causes of mortality within the study area (see Chapter 6) to examine whether any correlations might indicate causality. Finally, we recommend conservation actions to reduce the impact of the main drivers of territorial abandonment.

Methods

Study Area

The Bearded Vulture territories located in southern Africa during 2000-2012 (n=190) (see Krüger *et al.* 2014, Chapter 2) formed the baseline of this study. Of these, 109 territories were classified as occupied and 81 were classified as abandoned (Figure 3.1).

The location of the nest site within each territory was plotted using ArcGIS v.10.0 (ESRI, Redlands, USA). Where a pair had alternative nest sites on the territorial cliff, the location of the most frequently used site was plotted (see Krüger *et al.* 2014, Chapter 2). Around each nest site we created a buffer with a 10 km radius (314 km²) (Figure 3.1). These circles were based on the average 90% kernel density home range estimates for adults (286 km², 9.5 km radius; see

Chapter 4) and aimed to encapsulate the overall home range of a territorial pair, which was supported by the circles encompassing 92% (86–96%, $n=6$) of all GPS fixes obtained from satellite tagged adults (see Chapter 4). Although many of these buffer circles overlapped, this is realistic since foraging territories of the species are not exclusive with little intraspecific competition (Brown 1990, Margalida *et al.* 2003). Information for our covariates relating to human impact, food availability and climate change (detailed below) were quantified within these circles.

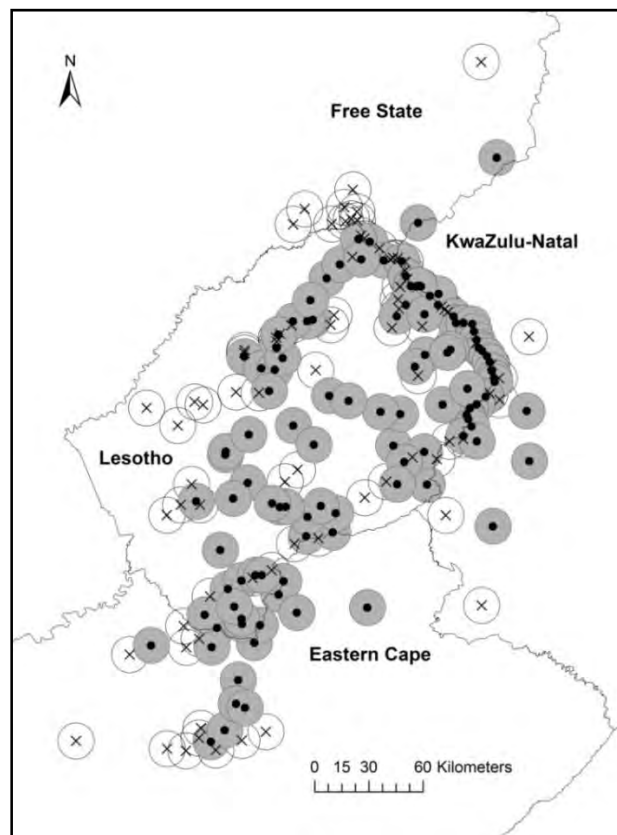


Figure 3.1 The location of breeding territories of the Bearded Vulture in southern Africa with occupied territories (●) surrounded by shaded 10 km radius buffers and abandoned (x) territories surrounded by open 10 km radius buffers.

Extraction of Covariates Surrounding Each Territory

Seven covariates representing the three hypotheses were used to describe the environment within a 10 km radius around each of 190 nest sites (Figure 3.2, Table 3.1). Information on

environmental variables was calculated in ArcGIS and the Geospatial Modelling Environment (GME) (Beyer 2012).

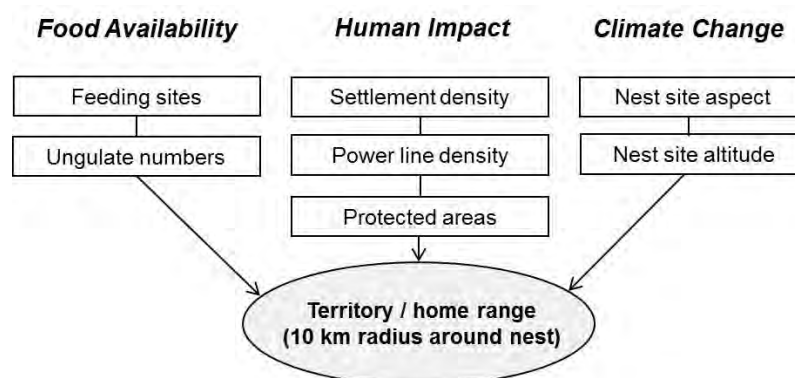


Figure 3.2 Conceptual model of the seven variables representing three hypotheses proposed to influence the abandonment of a territory by Bearded Vulture in southern Africa. For a description of all variables see Table 3.1.

Table 3.1 Variables used to characterize the area within a 10 km radius around the nest site representing the territory of a Bearded Vulture in southern Africa.

	Variable	Measure	Data Source
Food Availability	Feeding sites	Proximity index calculated based on supplementary feeding sites within a 76 km radius from the nest; $\sum(1/d^2)$, where d = the distance to the feeding site in km	Endangered Wildlife Trust and Ezemvelo KwaZulu-Natal Wildlife Vulture Restaurant Database, 2013
	Ungulate numbers	Total available biomass (number) of ungulates (livestock and wild ungulates)	Lehohla, 2002, Dzimba and Matooane 2005, 2012 Agricultural statistics ¹ , Ezemvelo KwaZulu-Natal Wildlife, South African National Parks, Free State Economic Development, Tourism and Environmental Affairs
Human Impact	Power lines	Total distance (km) of 11 kV, 22 kV and 132 kV power lines	South Africa: Eskom, 2012 Lesotho: Lesotho Electricity Corporation, 2013
	Settlements	Total number of buildings	South Africa: Eskom, 2013 Lesotho: Maloti Drakensberg Transfrontier Project, 2006
	Protected areas	Total area (in km ²) under formal protection	Maloti Drakensberg Transfrontier Project Database
Climate Change	Nest altitude	Altitude (m) of the nest cliff	1:50,000 topographical maps, GPS readings
	Nest aspect	Aspect (four cardinal directions) of the nest entrance	Field survey data

¹Directorate: Statistics and Economic Analysis of the Department of Agriculture, Forestry and Fisheries.

Three covariates were used to examine the *Human Impact* hypothesis: (i) Settlements: This was the density of human settlements measured as the total number of buildings surrounding each territory. (ii) Power lines: This was the density of power lines measured as the total length (in km) of low (11 kV), medium (22 kV) and high voltage (132 kV) power lines surrounding each territory. (iii) Protected areas: This was the area in km² under formal protection surrounding each territory. If human impacts were influencing territorial abandonment we predict that territories with higher human densities, more infrastructure and less protection, are more likely to have been abandoned.

Two covariates were used to examine the *Food Availability* hypothesis: (i) Predictable food resource (feeding sites): A proximity index was calculated based on the average maximum distance an adult would fly to a supplementary feeding site (76 km, *unpubl. data*) and the sum of reciprocals of the squared distance to each feeding site within a 76 km radius of the nest. We predict that if food shortage is a driver for abandonment, then those territories with a higher proximity index, *i.e.* those with more feeding sites closer to the nest, would be less likely to be abandoned. (ii) Unpredictable food resource (ungulate numbers): Food availability was estimated as the total number of ungulates surrounding each territory. These were calculated based on the type of land use surrounding each nest and the density of ungulates predicted to be in each habitat type. Numbers of ungulates were inferred from statistics available for livestock densities per district in Lesotho (Lehohla 2002, Dzimba and Matooane 2005) and per province in South Africa (2012 Agricultural statistics, Directorate: Statistics and Economic Analysis of the Department of Agriculture, Forestry and Fisheries), and from game count data available for wild ungulates in protected areas (Ezemvelo KwaZulu-Natal Wildlife; South African National Parks; Free State Economic Development, Tourism and Environmental Affairs; *unpubl. data*). Ungulate numbers were then calculated based on the proportion of open vegetation (Global land cover data 2009) and protected areas in each district/province (Ezemvelo KwaZulu-Natal Wildlife database) for livestock and wild ungulates respectively. To account for the transhumance of livestock in Lesotho, numbers in the highland regions in Lesotho were

halved. A positive relationship between the numbers of ungulates and availability of carcasses was assumed (*i.e.* more ungulates implies more carcasses available). If food shortages were important in driving territorial abandonment we predict that territories with an overall higher number of ungulates would be less likely to have been abandoned.

Two covariates were used to examine evidence that *Climate Change* may have influenced territorial abandonment: (i) Aspect: The direction of the nest entrance recorded as one of four cardinal directions based on field survey data. If climate change was an important factor influencing territorial abandonment we predict that nests facing north and east (*i.e.* with greatest exposure to the sun) will be most affected and therefore have a higher probability of being abandoned. (ii) Altitude: The altitude of the nest cliff was determined from field survey data or estimated from 1:50,000 topographical maps. We predict that if climate change is influencing abandonment then territories at lower altitudes, where temperatures would be higher, would be most likely to have been abandoned. Although ideally temperature change *per se* would also have been considered as a covariate, detailed climate data were not available at the nest site scale.

Statistical Analyses

We used Generalized Linear Models (GLiM) (binomial error structure and a logit link function) in R v.3.0.1 (R Core Team 2013) to explore associations between the occupancy status (occupied=1, abandoned=0) of each territory and the seven covariates. We ran models for all breeding territories in southern Africa and then separately for breeding territories in Lesotho (n=92) and South Africa (n=98).

We used model selection using Akaike's information criterion (AIC) and multi-model inference with the MuMIn v.1.9.13 package (Barton 2013) to determine which covariates were associated with territorial abandonment. We ranked models using their corrected AICc values and derived the Akaike weight of each model (w_i) estimated according to Burnham and Anderson (2002). Model suitability was assessed using AIC ranks and evidence ratios

(Whittingham *et al.* 2006, Lukacs *et al.* 2007) where the models with the highest weight and lowest evidence ratios were more important relative to others. We determined the change in AICc relative to the optimal model (Δ_i) and sub-setted all models with $\Delta_i < 2$. This method identifies the relative importance of different variables. Where there were competing models, the parameter estimates of each variable were calculated using model averaging and their 95% confidence limits obtained.

As a cross-validation of our models we computed the Receiver Operating Characteristic (ROC) curve using the package pROC v.1.7.2 (Robin *et al.* 2011). This method assesses the performance, and summarizes the overall appropriateness of the model (Nemes and Hartel 2010). The area under the curve (AUC) is a good numerical index (Hanley and McNeil 1982) and was thus used to summarize the ROC curve and to measure the performance of the model. Models with an AUC value > 0.5 have information about the response variable and possess a certain predictive power. Models with AUC values between 0.5 and 0.7 have low accuracy, between 0.7 and 0.9 have moderate and over 0.9 have high accuracy (Streiner and Cairney 2007). Therefore the higher the AUC value, the better the fit of the model. Low AUC values, however, do not necessarily indicate a poor model, rather they suggest that factors other than the predictor variables may also be influencing the response variable (Nemes and Hartel 2010).

Results

Data on nest site aspect were only available for 71% of the territories (n=89 occupied and n=46 abandoned). An initial analysis with this smaller sample size revealed that aspect did not feature in any of the top five models ($\Delta_i < 2$) and only featured within the top 14 (Appendix 3.1). Aspect also had by far the lowest relative importance value (Appendix 3.2). We therefore excluded aspect from further analyses thereby allowing a more comprehensive analysis using data from all 190 territories which had complete information for the other covariates.

Influence of Environmental Variables on Territorial Abandonment

Our models found strong support for an influence of power lines and settlements on territorial abandonment. All five of our best models (Table 3.2) included the influence of power lines and three of the top four models included settlements. Power lines and settlements had the highest relative importance score (1 and 0.72 respectively) and for power lines the confidence limits of the model averaged parameter estimate did not overlap zero (Table 3.3) and there was only very marginal overlap for settlements. Two other terms featured in our five top models, namely the percentage of area protected within a territory and the proximity to feeding sites. However, each variable only featured in one model within the best model subsets and their relative importance values were low (Table 3.3). Furthermore, for one of these terms (protected areas) the confidence limits of the model average parameter estimates overlapped zero.

Power line density and settlement density were more than twice as high surrounding abandoned territories compared with occupied ones (Figure 3.3). The relationship between territory occupancy and both power lines and settlements was negative, with the probability of occupancy decreasing with an increase in the density of power lines (Figure 3.4a) and settlements (Figure 3.4b). The model averaged parameter estimates from the best model subsets predicted a 5.6% increase in the probability of abandonment for each additional 10 km of power lines and an increase of 3.3% for each additional 500 settlements.

We found no support for altitude or ungulate numbers influencing occupancy with neither of these variables featuring in any of our top models (Table 3.2) suggesting that these variables did not differ greatly between abandoned and occupied territories (Figure 3.3).

Table 3.2 Results from the top 10 Generalized Linear Models testing for associations between territorial abandonment and altitude, density of human settlements and power lines, percentage of protected areas, feeding site proximity and the number of ungulates within a 10 km radius around the nest site (n=190 nests; 109 occupied and 81 abandoned). Headers for columns are: number of parameters (K), change in AICc relative to the optimal model (Δ_i), AICc weight (w_i) and evidence ratio (ER). The top models (*i.e.* those with $\Delta_i < 2$) are shown in bold.

Intercept	Altitude	Ungulate numbers	Feeding sites	Protected areas	Settlements	Power lines	K	Δ_i	w_i	ER
0.8014					-0.000298	-0.024760	3	0.00*	0.24	
0.724						-0.026190	2	0.75	0.16	1.50
0.8382				-0.000728	-0.000299	-0.025090	4	1.97	0.09	2.67
0.8172			-1.860000		-0.000291	-0.024570	4	1.98	0.09	2.67
0.8439		-8.255 e ⁻⁰⁹			-0.000299	-0.024510	4	2.06	0.09	2.67
0.814	-0.000005				-0.000299	-0.024790	4	2.09	0.08	3.00
0.752			-2.994000			-0.025770	3	2.52	0.07	3.43
0.761				-0.000732		-0.026500	3	2.69	0.06	4.00
0.7499		-5.053 e ⁻⁰⁹				-0.026050	3	2.80	0.06	4.00
0.6814	0.000016					-0.026060	3	2.81	0.06	4.00

*The optimal model had an AICc value of 243.

Table 3.3 Model parameter estimates for each variable measured within a 10 km radius around the nest site averaged across the top four models, with the 95% confidence limits of the estimate and the relative importance of each term within those models.

Variable	Parameter estimate	Confidence limits		Relative importance
		2.5%	97.5%	
Intercept	0.787514	0.0039270	1.182326	
Power lines	-0.025183	-0.039433	-0.010933	1.00
Settlements	-0.000297	-0.000668	0.000074	0.72
Protected areas	-0.000728	-0.004947	0.003492	0.15
Feeding sites	-1.859512	-0.133396	-9.620571	0.15

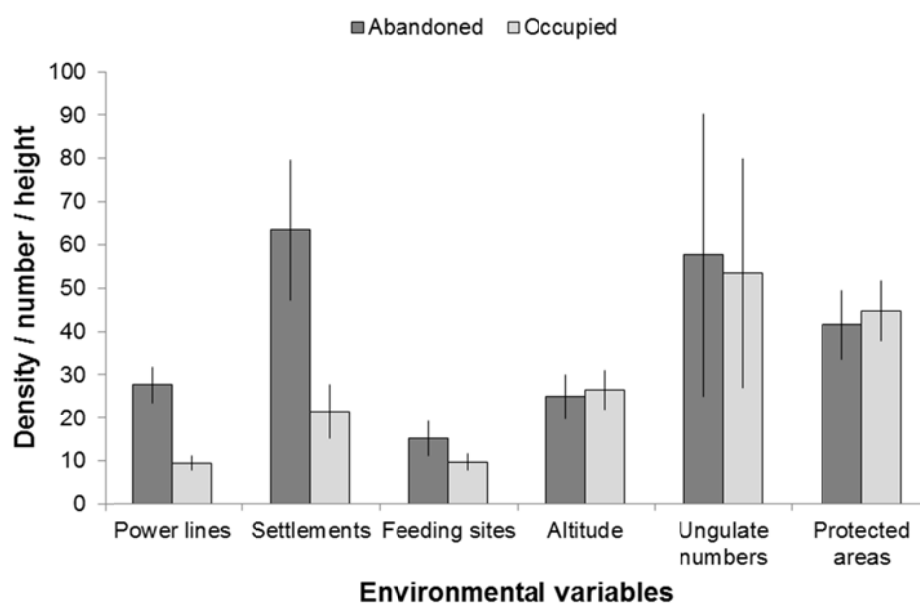


Figure 3.3 Comparison between the average (mean \pm SE) density of human impacts (power lines and settlements), feeding site proximity, altitude, number of ungulates and percentage of area protected within a 10 km radius around nest sites of abandoned and occupied territories indicating that abandoned sites had a higher density of human impacts, higher feeding site proximity index and lower percentage of area protected whereas there was little difference in the altitude of nests sites or the number of ungulates within the territory. Values have been adjusted for display purposes (settlements \times 0.1; feeding sites \times 10,000; altitude \times 0.1; ungulate numbers \times 0.001).

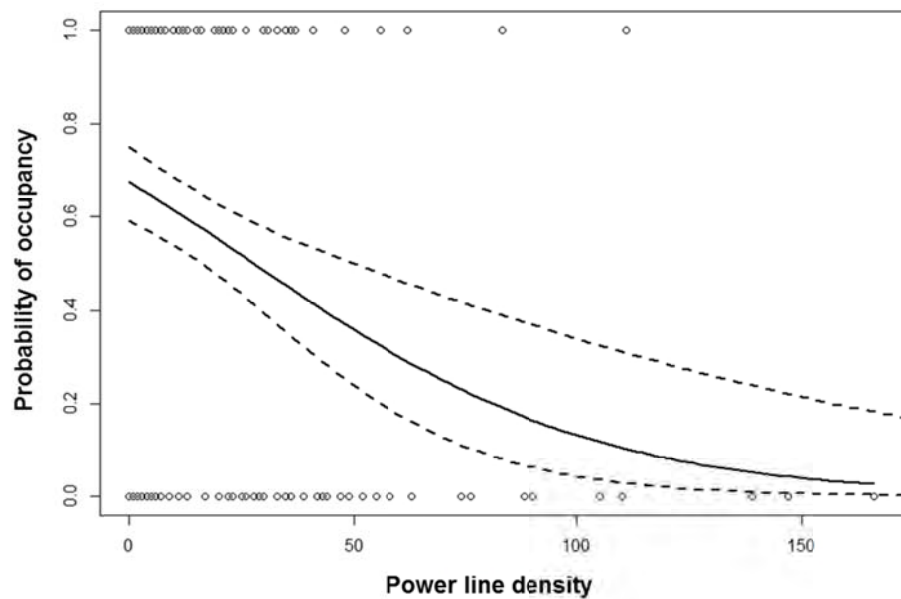


Figure 3.4a The relationship between the probability of territory occupancy (where '0' is abandoned and '1' is occupied) and the density of power lines. The line is the fitted line from a Binomial Generalized Linear Model. The probability of occupancy decreases with an increase in the total distance of power lines within the 10 km radius around nest sites.

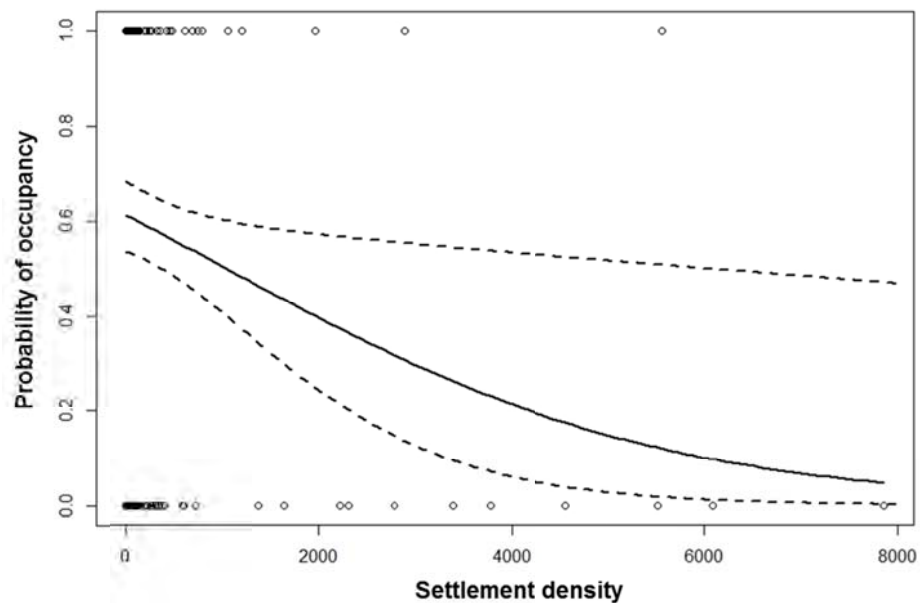


Figure 3.4b The relationship between the probability of territory occupancy (where '0' is abandoned and '1' is occupied) and the density of settlements. The line is the fitted line from a Binomial Generalized Linear Model. The probability of occupancy decreases with an increase in the total number of buildings within the 10 km radius around nest sites.

Analyzing Lesotho and South African territories separately, our models suggested that the variables associated with abandonment in each country were similar to those in the two countries combined. South Africa showed a similar result to the overall models with the most support for power lines and settlements; power lines were present in all five top models and settlements in all but one (Table 3.4). Both variables had high relative importance scores of 1 and 0.84 respectively (Appendix 3.3). In Lesotho there were many more plausible models (nine models with $\Delta_i < 2$), however, once again power lines and settlements received the most support, featuring in seven and six of the top nine models respectively (Table 3.5); additionally feeding sites also featured in six of the top nine models. For Lesotho, all three of these factors had similar relative importance scores (between 0.70 and 0.78) (Appendix 3.4). As before, power line and settlement density were negatively related to occupancy, whereas feeding sites were positively related with a higher feeding site proximity index at occupied sites.

Our overall model had an AUC value of 0.69, and the models for South Africa and Lesotho had AUC values of 0.70 and 0.68 respectively. The models were all of similar accuracy, and were classified as a poor to moderate fit or of low to medium accuracy (Streiner and Cairney 2007). The performance of our models suggests that there are other factors over and above the hypotheses we tested contributing to territorial abandonment.

Table 3.4 Results from the top 10 Generalized Linear Models testing for associations between territorial abandonment and altitude, density of human settlements and power lines, percentage of protected areas, feeding site proximity and the number of ungulates within a 10 km radius of nest sites in South Africa (n=98 nests, 44 occupied and 54 abandoned). Headers for columns are: number of parameters (K), change in AICc relative to the optimal model (Δ_i), AICc weight (w_i) and evidence ratio (ER). The top models (*i.e.* those with $\Delta_i < 2$) are shown in bold.

Intercept	Altitude	Ungulate numbers	Feeding sites	Protected areas	Settlements	Power lines	K	Δ_i	w_i	ER
0.943200					-0.00034	-0.02447	3	0.00*	0.15	
1.347000				-0.00356	-0.00040	-0.0287	4	0.60	0.11	1.36
0.521100		1.39 e⁻⁰⁷			-0.00042	-0.02926	4	0.62	0.11	1.36
0.762800						-0.0257	2	1.16	0.09	1.67
1.044000			-6.939		-0.00033	-0.02383	4	1.22	0.08	1.88
0.284100	0.000231				-0.00033	-0.02179	4	2.06	0.06	2.50
0.872800			-7.319			-0.02479	3	2.13	0.05	3.00
0.648300		1.23 e ⁻⁰⁷	-5.256		-0.00041	-0.02815	5	2.31	0.05	3.00
1.374000			-5.054	-0.00313	-0.00039	-0.02773	5	2.32	0.05	3.00
-0.840200	0.000457	1.57 e ⁻⁰⁷			-0.00041	-0.02446	5	2.44	0.05	3.00

*The optimal model had an AICc value of 124.6

Table 3.5 Results from the top 10 Generalized Linear Models testing for associations between territorial abandonment and altitude, density of human settlements and power lines, percentage of protected areas, feeding site proximity and the number of ungulates within a 10 km radius of each nest site in Lesotho (n=92 nests, 37 occupied and 55 abandoned). Headers for columns are: number of parameters (K), change in AICc relative to the optimal model (Δ_i), AICc weight (w_i) and evidence ratio (ER). The top models (*i.e.* those with $\Delta_i < 2$) are shown in bold.

Intercept	Altitude	Ungulate numbers	Feeding sites	Protected areas	Settlements	Power lines	K	Δ_i	w_i	ER
1.027000			91.22		-0.011880	-0.022510	4	0.00*	0.12	
0.729100			126.50		-0.012400		3	0.45	0.09	1.33
1.377000					-0.011960	-0.028940	3	0.71	0.08	1.50
0.313100			106.70			-0.022330	3	0.79	0.08	1.50
2.654000		-0.000557	86.71		-0.014910	-0.024290	5	1.24	0.06	2.00
3.455000		-0.000714			-0.016160	-0.030690	4	1.33	0.06	2.00
-0.038890			147.60				2	1.74	0.05	2.40
0.702400						-0.02893	2	1.76	0.05	2.40
0.966200			85.06	0.009202	-0.011020	-0.02333	5	1.98	0.04	3.00
1.870000	0.000401		126.50		-0.01458		4	2.05	0.04	3.00

*The optimal model had an AICc value of 120.7

Discussion

Our analyses represent an attempt to empirically assess the evidence for drivers of territorial abandonment of the Bearded Vulture in southern Africa by using variables related to three different hypotheses. Our models provide strongest support for the hypothesis that anthropogenic activities may be driving territorial abandonment, with a small degree of support for the hypothesis that food shortages were important and no support at all for the hypothesis that abandonment has been driven by climate change. The performance of our overall model was similar to the accuracy of the models at a home range scale for Egyptian Vultures *Neophron percnopterus* (0.71-0.74) fitted by Mateo-Tomás and Olea (2010).

Across all analyses there was considerable support for an association between nest abandonment and (i) power line density and (ii) human settlements; territories that were abandoned had over twice the density of power lines and human settlements surrounding them than territories that remained occupied. The fact that many of the supported models included both these terms suggests that the association between these variables was not simply due to a correlation between these variables, but that both variables were independently associated with abandonment. These patterns were also present from the country-specific analyses, with support for these variables present in both the South African and the Lesotho analyses. This result further suggests that these associations were not simply the result of an association in only one location, but appeared to be a more general pattern occurring across regions.

Although our results are correlational, support for our anthropogenic activity hypothesis also comes from other lines of evidence. For example, causes of mortality of Bearded Vulture carcasses collected in the study area over a similar time period indicated that death was almost entirely as a result of anthropogenic factors with more than half being attributed to indirect and accidental poisoning and persecution, and almost a quarter to power line collisions (see Chapter 6). Similarly non-natural mortalities attributed to illegal poisoning were the main mortality factors in other Bearded Vulture populations (Margalida *et al.* 2008) and other large

raptor populations (Whitfield *et al.* 2004, Smart *et al.* 2010, Virani *et al.* 2010), and collisions with power lines are known to threaten other vulture species in Africa (Smallie and Virani 2010, Boshoff *et al.* 2011). Impacts related to human disturbance were also found to limit the distribution patterns of Bearded Vulture and other large raptor populations in terms of their breeding ranges and densities (Brown 1988, Donazar *et al.* 2002, Margalida *et al.* 2007) and their foraging areas (Herremans and Herremans-Tonnoyer 2000, Bautista *et al.* 2004, Gavashelishvili and McGrady 2006).

There was only very limited support for our hypothesis that food shortages could have driven territorial abandonment. In mountainous regions with extensive stock rearing, the livestock death rate is high due to the high incidents of accidents, theft, predation and poor veterinary care (Newton 1979). This is particularly true for the communal rangelands in Lesotho, therefore food shortages would not be expected in this country. Food shortages would also not be expected in South Africa because of a number of regularly provisioned supplementary feeding sites in this country. In Lesotho our country-specific model suggested that feeding sites may play an important role in maintaining territorial occupancy. However, this result might be questionable, since there are only two feeding sites in Lesotho and these are provisioned on an irregular basis. Thus, our findings may simply be a result of the location of occupied territories in the mountainous areas close to the South African border where birds have better access to feeding sites. Abandoned territories appear more frequent in western Lesotho which is more developed as a result of the accessible terrain and therefore may experience higher human impacts, but is further away from the feeding sites in South Africa. Although territories in Lesotho could benefit from the establishment of supplementary feeding sites which are regularly provisioned, this action does not seem to be a priority considering our overall results which suggest that territorial abandonment is unlikely to be driven by food shortages. These results do not, however, demonstrate whether food shortages are influencing productivity or recruitment through non-adult survival and these aspects still merit further research on their role in the decline of the population.

Our models provide no support for the previously proposed hypothesis that territorial abandonment might be driven by climate change— specifically increases in temperatures (Colahan and Esterhuizen 1997, Simmons and Jenkins 2007). Territories that were at lower altitudes and therefore more likely to experience higher temperatures were not significantly more likely to be abandoned, nor were territories with hotter nest site aspects (*i.e.* sites facing east and north). Therefore these results do not suggest that global warming has directly lead to territorial abandonment, although this does not necessarily mean that these changes aren't influencing other aspects of the species' demography such as productivity or survival, and timing of breeding.

Information provided in this chapter raises the question of whether the continued decline of the species is in response to unnatural mortality factors as suggested by our models, or low breeding success/recruitment or a combination of these. Several studies have found human activities to influence breeding success (Donázar *et al.* 1993, Margalida *et al.* 2003) and breeding pairs are known to prefer more isolated areas with low levels of human activity (Brown 1988). Brown (1990) found the breeding success of this population to be high (0.89 young per pair per year) but current evidence (see Chapter 6) suggests that productivity may have decreased by about 40% since Brown's (1990) study. We recommend that further studies focus on establishing whether breeding success and low recruitment are limiting factors for this population. With the expansion of human activities into core breeding areas, we can expect lowered breeding success and ultimately nest abandonment. In addition, there may be a lack of adaptation to the conditions found in the periphery of the range, as shown for harriers (García and Arroyo 2001), which may affect breeding success.

With few non-breeding adults in the population (Krüger *et al.* 2014, Chapter 2), a small proportion of sub-adults that face a high risk of exposure to human impacts (see Chapter 4), and high mortality rates (see Chapter 6), vacant territories are unlikely to become occupied. As a result, the population may be shrinking back to their preferred habitat with sub-optimal territories being abandoned as suggested in Chapter 2. Results from Chapter 2 also show that

territories in the periphery of the range were more likely to be abandoned. We intentionally did not include territory location (*i.e.* periphery score) as a covariate in our models because we expected this variable would be correlated with many of our covariates and we were potentially interested in the mechanism involved and not merely the pattern. However, in a post-hoc analysis we found that the territory location variable was not amongst the top models (those with $\Delta_i < 2$). This suggests therefore that our relationships were not simply the result of a shrinkage of the population back to the core of the range and actually further strengthens our human impact hypothesis.

Based on the identified threats and mechanisms of abandonment, we recommend conservation management to focus on actions that will limit increased human densities and associated developments and influence the attitudes of people living within the territories of breeding pairs. We recommend that mitigation of existing power lines, stricter scrutiny of development proposals and proactive engagement with developers to influence the placement of structures is essential within the home range of a territorial pair.

For management to be effective however, both the breeding range (as discussed here) and foraging range of the population must be taken into account (Donazar *et al.* 1993, Carrete and Donazar 2005). We recommend that the potential threats posed by power lines and human settlements identified in this study, be investigated within the foraging range of non-adults to ensure a more holistic approach to the management of the species, since non-adults form a large proportion of the population (Newton 1979, Brown *et al.* 1982) and conservation measures designed to protect breeding birds only may not be sufficient to safeguard the population as a whole (Penteriani *et al.* 2005, Gonzalez *et al.* 2006).

Our use of multiple models to investigate a number of alternate hypotheses has provided insight into the mechanisms of decline and those variables affecting territory occupancy. Investigating these mechanisms at a regional level also provides the necessary information to target actions appropriately. Our study approach and findings are likely to be of considerable

interest to those studying vulture declines, which is increasingly being recognised as one of the most pressing issues in avian conservation globally and particularly in Africa.

Acknowledgements

Nick Liebenberg, University of Cape Town, is thanked for his assistance in quantifying the environmental variables within the 190 territories in ArcGIS. The Lesotho Electricity Corporation provided power line distribution data and Eskom provided power line and settlement data. Bimall Naidoo, Ezemvelo KwaZulu-Natal Wildlife, is thanked for her assistance in obtaining the Eskom data.

References

- Amar A, Redpath S, Sim I and Buchanan G (2010) Spatial and temporal associations between recovering populations of common raven *Corvus corax* and British upland wader populations. *J Appl Ecol* 47: 253-262.
- Barton K (2013) MuMIn: Multi-model inference R package version 1.9.13. <http://CRAN.R-project.org/package=MuMIn>.
- Bautista LM, García JT, Calmaestra MG, Palacín C, Martín CA, Morales MB, Bonal R and Viñuela J (2004) Effect of weekend road traffic on the use of space by raptors. *Conserv Biol* 18: 726-732.
- Beyer HL (2012) Geospatial Modelling Environment (Version 0720) (software). URL: <http://wwwspatialecology.com/gme>.
- BirdLife International (2014) IUCN Red List for birds. Downloaded from <http://www.birdlife.org> on 05/08/2014.

- Boshoff A, Minnie JC, Tambling CJ and Michael MD (2011) The impact of power line-related mortality on the Cape Vulture *Gyps coprotheres* in a part of its range, with an emphasis on electrocution. *Bird Cons Int* 21:311-327.
- Brown CJ (1988) A study of the Bearded Vulture *Gypaetus barbatus* in southern Africa. Dissertation, University of Natal, Pietermaritzburg.
- Brown CJ (1990) Breeding biology of the Bearded Vulture in southern Africa, Parts I – III. *Ostrich* 61: 24-49
- Brown CJ (1991) An investigation into the decline of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Biol Conserv* 57: 315-337.
- Brown CJ (1997) Population dynamics of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Afr J Ecol* 35: 53-63.
- Brown LH, Urban E and Newman K (1982) Birds of Africa Vol 1. Academic Press, Orlando, Florida.
- Buchanan GM, Pearce-Higgins JW, Wotton SR, Grant MC and Whitfield DP (2003) Correlates of the change in Ring Ouzel *Turdus torquatus* abundance in Scotland from 1988–91 to 1999. *Bird Study* 50: 97–105.
- Burnham KP and Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York.
- Butchart SHM *et al.* (2010) Global Biodiversity: Indicators of Recent Declines. *Science* 328: 1164.
- Carrete M and Donazar JA (2005) Application of central-place foraging theory shows the importance of Mediterranean dehesas for the conservation of the Cinereous Vulture, *Aegypius monachus*. *Biol Conserv* 126: 582–590.

- Caughley G (1994) Directions in Conservation Biology. *J Anim Ecol* 63: 15–244.
doi:102307/5542.
- Colahan BD and Esterhuizen JR (1997) The status and conservation of vultures in the Free State Province, South Africa. In: Boshoff AF *et al.* (editors). Vultures in the 21st Century: Proceedings of a Workshop on Vulture Research and Conservation in Southern Africa. Vulture Study Group, Johannesburg, pp. 46-49.
- Convention on Biological Diversity, Montréal (2010) Secretariat of the Convention on Biological Diversity 2010. Global Biodiversity Outlook 3.
- Cortez-Avazida A, Carrete M and Donázar JA (2010) Managing supplementary feeding for avian scavengers: guidelines for optimal design using ecological criteria. *Biol Conserv* 143: 1707-1715.
- DeSalle R and Amato G (2004) The expansion of conservation genetics. *Nat Rev Genet* 5: 702–712.
- Deygout C, Gault A, Sarrazin F and Bessa-Gomes C (2009) Modelling the impact of feeding stations on vulture scavenging service efficiency. *Ecol Modell* 220: 1826-1835.
- Donázar JA, Hiraldo F and Bustamante J (1993) Factors Influencing Nest Site Selection, Breeding Density and Breeding Success in the Bearded Vulture (*Gypaetus barbatus*). *J Appl Ecol* 30: 504-514.
- Donázar JA, Blanco G, Hiraldo F, Soto-Largo E and Oria J (2002) Effects of forestry and other land use practices on the conservation of Cinerous Vultures. *Ecol Appl* 12: 1145-1456.
- Dzimba J and Matooane M (2005) Stock theft as a threat to human security in Lesotho. In: Kariri JN and Mistry D (editors) Stock Theft and Human Security A Case Study of Lesotho. Lesotho Institute of Public Administration and Management (LIPAM), *unpubl report*, 89 pp.

- Energy Sector Policy of the AfDB Group (2012) African Development Bank Operational Resources and Policies Department (ORPC).
- Erasmus BFN, van Jaarsveld A, Chown SL, Kshatriya M and Wessels KJ (2002) Vulnerability of South Africa animal taxa to climate change. *Glob Change Biol* 8:679–693.
- García JT and Arroyo BE (2001) Effect of abiotic factors on reproduction in the centre and periphery of breeding ranges: a comparative analysis in sympatric harriers. *Ecography* 24: 393-402.
- Gavashelishvili A and McGrady MJ (2006) Breeding site selection by bearded vulture (*Gypaetus barbatus*) and Eurasian Griffon (*Gyps fulvus*) in the Caucasus. *Anim Conserv* 9: 159-170.
- González LM, Arroyo BE, Margalida A, Sanchez R and Oria J (2006) Effect of human activities on the behaviour of breeding Spanish Imperial Eagles (*Aquila adalbertz*): management implications for the conservation of a threatened species. *Anim Conserv* 9: 85-93.
- Green RE, Newton I, Schultz S, Cunningham AA, Gilbert M, Pain DJ and Prakash V (2004) Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. *J Appl Ecol* 41: 793–800.
- Hanley JA and McNeil BJ (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology* 142: 29-36.
- Heller NE and Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biol Conserv* 142: 14–32.
- Heredia R (1991) Chapter 2 Biología de la Reproducción. In: Heredia R, Heredia B (editors) El Quebrantahuesos (*Gypaetus barbatus*) en los Pirineos. ICONA, Madrid.
- Herremans M and Herremans-Tonnoyer D (2000) Land use and the conservation status of raptors in Botswana. *Biol Conserv* 94: 31–41.

- Hiraldo F, Delibes M and Calderon J (1979) El Quebrantahuesos: sistematica, taxonomia, biologia, distrubucion y proteccion. Monografias 22, ICONA, Madrid.
- Hoffmann M *et al.* (2010) The impact of conservation on the status of the world's vertebrates. *Science* 330: 1503–1509.
- Hulme M (1996) Recent climatic change in the world's drylands. *Geophys Res Lett* 23: 61-64.
- Huntley B and Barnard P (2012) Potential impacts of climatic change on southern African birds of fynbos and grassland biodiversity hotspots. *Divers Distrib* 18(8): 769-781.
- Huntley B, Altwegg R, Barnard P, Collingham YC and Hole DG (2012) Modelling relationships between species spatial abundance patterns and climate. *Glob Ecol Biogeogr* 21(6): 668-681.
- IPCC (2014) Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Barros *et al.* (editors). Cambridge University Press, Cambridge, United Kingdom and New York.
- Kalipeni E (editor) (1994) Population Growth and Environmental Degradation in Africa, 236 pp.
- Kruger AC and Sekele SS (2012) Trends in extreme temperature indices in South Africa: 1962–2009. *Int J Climatol* 33: 661-673. doi:10.1002/joc.3455.
- Krüger S (*in press*) Bearded Vulture. In Taylor MR (editor) The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. BirdLife South Africa, Johannesburg.
- Krüger S, Piper S, Rushworth I, Botha A, Daly B, Allan D, Jenkins A, Burden D and Friedmann Y (editors) (2006) Bearded Vulture (*Gypaetus barbatus meridionalis*) Population and Habitat Viability Assessment Workshop Report. Conservation Breeding Specialist Group (SSC/IUCN)/CBSG Southern Africa, Endangered Wildlife Trust, Johannesburg.

- Krüger SC, Allan DG, Jenkins AR and Amar A (2014) Trends in territory occupancy, distribution and density of the Bearded Vulture *Gypaetus barbatus meridionalis* in southern Africa. *Bird Cons Int* 24: 162-177. doi:101017/S0959270913000440.
- Lehman RN, Kennedy PL and Savidge JA (2007) The state of the art in raptor electrocution research: a global review. *Biol Conserv* 126: 159-174.
- Lehohla P (2002) Report on the survey of large and small scale agriculture Statistics, South Africa. Pretoria, South Africa, *unpubl report*, 115 pp.
- Lewis AJG, Amar A, Cordi-Piec D and Thewlis RMT (2007) Factors influencing Willow Tit *Poecile montanus* site occupancy: a comparison of abandoned and occupied woods. *Ibis* 149: 205-213.
- Lukacs PM, Thompson WL, Kendall WL, Gould WR, Doherty PF, Nurnham KP and Anderson, DR (2007) Concerns regarding a call for pluralism of information theory and hypothesis testing. *J Appl Ecol* 44: 456–460.
- Maphisa DH (1997) Vultures in Lesotho: past, present and future In: Boshoff AF *et al.* (editors) Vultures in the 21st Century: Proceedings of a Workshop on Vulture Research and Conservation in Southern Africa. Vulture Study Group, Johannesburg, South Africa, pp. 93-96.
- Mander M, Diederichs N, Ntuli L, Khulile M, Williams V and McKean S (2007) Survey of the Trade in Vultures for the Traditional Health Industry in South Africa. Futureworks, *unpubl report*, 30pp.
- Margalida A, Canut J and García D (2003) Territory change and Nest-site switching in the Bearded Vulture (*Gypaetus barbatus*). *J Raptor Res* 37(4): 333-337.

- Margalida A, García D and Cortés–Avizanda A (2007) Factors influencing the breeding density of Bearded Vultures, Egyptian Vultures and Eurasian Griffon Vultures in Catalonia (NE Spain): management implications. *Anim Biodiv Conserv* 30(2): 189–200.
- Margalida A, Heredia R, Razin M and Hernandez M (2008) Sources of variation in mortality of the Bearded Vulture *Gypaetus barbatus* in Europe. *Bird Cons Int* 18: 1-10.
- Mateo-Tomás P and Olea PP (2010) Diagnosing the causes of territory abandonment by the Endangered Egyptian vulture *Neophron percnopterus*: the importance of traditional pastoralism and regional conservation. *Oryx* 44: 424–433.
- Midgley G, Rutherford M and Bond W (2001) The heat is on: impacts of climate change on plant diversity in South Africa. National Botanic Institute, Cape Town, South Africa.
- Mingozzi T and Estève R (1997) Analysis of a historical extirpation of the Bearded vulture *Gypaetus barbatus* (L) in the Western Alps (France-Italy): former distribution and causes of extirpation. *Biol Conserv* 79: 155-171.
- Mokotjomela T, Schwaibold U and Pillay N (2010) Population surveys of the ice rat *Otomys sloggetti robertsi* in the Lesotho Drakensberg. *Afr Zool* 45:225–232.
- Mundy P, Butchart D, Ledger J and Piper S (1992) The Vultures of Africa. Russel Friedman Books CC, Johannesburg, South Africa.
- Nemes S and Hartel T (2010) Summary measures for binary classification systems in animal ecology. *North West J Zool* 6: 323-330.
- Newton I (1979) Population Ecology of Raptors. T and AD Poyser, Berkhamsted.
- Oaks *et al.* (2004) Diclofenac residues as the cause of vulture population decline in Pakistan. *Nature* 427: 630-633.

- Ogada DL, Keesing F and Virani MZ (2012) Dropping dead: causes and consequences of vulture population declines worldwide. *Ann NY Acad Sci* 1249: 57-71.
- Penteriani V, Otalora F, Sergio F and Ferrer M (2005) Environmental stochasticity in dispersal areas can explain the 'mysterious' disappearance of breeding populations. *Proc R Soc B* 272: 1265-1269. doi:101098/rspb20053075.
- Phipps WL, Willis SG, Wolter K and Naidoo V (2013) Foraging Ranges of Immature African White-Backed Vultures (*Gyps africanus*) and Their Use of Protected Areas in Southern Africa. *PLoS ONE* 8: e52813. doi:101371/journalpone0052813.
- Piper SE (2005) Supplementary feeding programmes: how necessary are they for the maintenance of numerous and healthy vulture populations? In: Houston DC and Piper SE (editors) *Conservation and Management of Vulture Populations*. Thessaloniki, Greece, pp. 41-50.
- R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria URL <http://www.R-project.org>.
- Robin X, Turck N, Hainard A, Tiberti N, Lisacek F, Sanchez J-C and Müller M (2011) pROC: an open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinform* 12: 77. doi:101186/1471-2105-12-77 <http://www.biomedcentral.com/1471-2105/12/77>.
- Sekercioglu CH, Daily GC and Ehrlich PR (2004) Ecosystem consequences of bird declines. *Proc Nat Acad Sci* 101: 18042–18047.
- Siegfried WR, Frost PGH, Cooper J and Kemp AC (1976) South African Red Data Book- Aves. South African National Science Programme Report No 7.
- Simmons RE, Barnard P, Dean WRJ, Midgley GF, Thuiller W and Hughes G (2004) Climate change and birds: perspectives and prospect from southern Africa. *Ostrich* 75: 295-308.

- Simmons, RE and Jenkins AR (2007) Is climate change influencing the decline of Cape and Bearded Vultures in southern Africa? *Vulture News* 56: 41-51.
- Smallie J and Virani MZ (2010) A preliminary assessment of the potential risks from electrical infrastructure to large birds in Kenya. *Scopus* 30: 32–39.
- Smart J, Amar A, Sim IMW, Etheridge B, Cameron D and Christie G (2010) Illegal killing slows population recovery of a re-introduced raptor of high conservation concern – The red kite *Milvus milvus*. *Biol Conserv* 143: 1278–1286.
- Streiner DL and Cairney J (2007): What's under the ROC? An introduction to Receiver Operating Characteristic Curves. *Can J Psychiatr* 52:121-128
- Thiollay J-M (2007) The decline of raptors in west Africa: long-term assessment and the role of protected areas. *Ibis* 148:240–254.
- Thomas CD, Cameron, A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFM, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, Midgley, GF and Williams SE (2004) Extinction risk from climate change. *Nature* 427: 145-148.
- Virani MZ, Kendall C, Njoroge P and Thomsett S (2010) Major declines in the abundance of vultures and other scavenging raptors in and around the Masai Mara ecosystem, Kenya. *Biol Conserv* 144: 746–752.
- Whitfield DP, Fielding AH, Mcleod DRA and Haworth PF (2004) Modelling the effects of persecution on the population dynamics of golden eagles in Scotland. *Biol Conserv* 119: 319–333.
- Whittingham MJ, Stephens PA, Bradbury RB and Freckleton RP (2006) Why do we still use stepwise modelling in ecology and behaviour? *J Anim Ecol* 75: 1182-1189.
- Xirouchakis S, Sakoulis A and Andreou G (2001) The decline of the Bearded Vulture *Gypaetus barbatus* in Greece. *Ardeola* 48(2): 183-190.

Appendices

Appendix 3.1 Results from the 14 GLiM models testing for associations between territorial abandonment (n=135 nests) and altitude, density of human settlements and power lines, percentage of protected areas, feeding site proximity and the number of ungulates within a 10 km radius around the nest site. Headers for columns are: number of parameters (K), change in AICc relative to the optimal model (Δ_i), AICc weight (w_i) and the evidence ratio (ER). The top models (*i.e.* those with $\Delta_i < 2$) are shown in bold.

Intercept	Aspect	Altitude	Ungulate numbers	Feeding sites	Protected areas	Settlements	Power lines	K	Δ_i	w_i	ER
1.2520						-0.000387	-0.028390	3	0*	0.14	
1.4310				-18.750000		-0.000342	-0.028650	4	0.57	0.1	0.04
1.4500					-0.002914	-0.000397	-0.030230	4	0.69	0.1	0.04
0.9601			6.50 e⁻⁰⁸			-0.000391	-0.031140	4	1.26	0.07	0.04
1.3490				-22.520000			-0.029080	3	1.53	0.06	0.05
1.1180							-0.029340	2	2.04	0.05	0.07
0.9830		9.82 e ⁻⁰⁵				-0.000385	-0.027500	4	2.08	0.05	0.04
1.4740				-10.440000	-0.001824	-0.000363	-0.029550	5	2.39	0.04	0.03
1.2520			3.02 e ⁻⁰⁸	-14.230000		-0.000351	-0.029750	5	2.6	0.04	0.03
0.8873		2.11 e ⁻⁰⁴			-0.003145	-0.000395	-0.028450	5	2.64	0.04	0.03
1.2090		8.07 e ⁻⁰⁵		-18.770000		-0.000341	-0.027920	5	2.7	0.04	0.03
1.3010					-0.002725		-0.031000	3	2.82	0.03	0.05
1.4290			3.39 e ⁻⁰⁹		-0.002823	-0.000396	-0.030320	5	2.85	0.03	0.03
1.2400	+					-0.000402	-0.029460	6	3.15	0.03	0.02

*The top model had an AICc value of 162.7

Appendix 3.2 Model parameter estimates for each variable measured within a 10 km radius around the nest averaged across the top nine models, with the 95% confidence limits of the estimate and the relative importance of each term within those models.

Variable	Parameter estimate	Confidence limits		Relative importance
		2.5%	97.5%	
Intercept	1.238000	-0.094608	2.570009	
Power lines	-0.029380	-0.049071	-0.009692	1.00
Settlements	-0.000379	-0.000782	0.000025	0.76
Feeding sites	-18.600000	-60.416470	23.222620	0.38
Protected areas	-0.002658	-0.008307	0.002991	0.29
Ungulate numbers	0.000000	0.000000	0.000000	0.22
Altitude	0.000132	-0.000762	0.001025	0.17
Aspect N	0.018070	-1.172902	1.209051	0.08
Aspect S	0.092600	-1.066834	1.252040	0.08
Aspect W	-2.049000	-4.617562	0.519971	0.08

Appendix 3.3 Model parameter estimates for each variable measured within a 10 km radius around each nest in South Africa (n=98) averaged across the top five models, with the 95% confidence limits of the estimate and the relative importance of each term within those models.

Variable	Parameter estimate	Confidence limits		Relative importance
		2.5%	97.5%	
Intercept	0.927500	0.021339	1.833587	
Power lines	-0.026420	-0.045174	-0.007673	1.00
Settlements	-0.000372	-0.000786	0.000043	0.84
Protected areas	-0.003561	-0.009271	0.002148	0.21
Ungulate numbers	0.00000014	-0.000000086	0.000000037	0.20
Feeding sites	-6.939000	-0.232973	9.418740	0.15

Appendix 3.4 Model parameter estimates for each variable measured within a 10 km radius around each nest site in Lesotho (n=92) averaged across the top six models, with the 95% confidence limits of the estimate and the relative importance of each term within those models.

Variable	Parameter estimate	Confidence limits		Relative importance
		2.5%	97.5%	
Intercept	1.21900	-1.42006	3.85849	
Power lines	-0.02548	-0.05552	0.00456	0.78
Settlements	-0.01289	-0.02748	0.00169	0.72
Feeding sites	106.40000	-53.31684	266.02830	0.70
Altitude	-0.00063	-0.00182	0.00055	0.19
Protected areas	0.00920	-0.02934	0.04774	0.07

Chapter 4: Differential range use and anthropogenic risk exposure between age classes of southern African Bearded Vultures *Gypaetus barbatus*



Photo 4 Adult Bearded Vulture with a solar-powered GPS satellite transmitter

A modified form of this chapter has been accepted by PLoS ONE and is currently in press:

Krüger SC, Reid T and Amar A (*in press*) Differential range use between age classes of southern African Bearded Vultures *Gypaetus barbatus*.

Abstract

Bearded Vulture *Gypaetus barbatus* movements were investigated in southern Africa to determine whether an individual's age, sex or breeding status influenced its exposure to perceived benefits (e.g. supplementary feeding sites or protected areas) or anthropogenic risks (e.g. power lines, settlements or roads). Data from satellite transmitters fitted to 18 individuals of four age classes were used to determine range size and use. Because of the nature of the species' movements, these data could be used to determine the overall foraging range of the population, which was estimated to be 51,767 km². Although juvenile, immature and sub-adult birds used different parts of the overall range, their combined foraging range was 65% (33,636 km²) of the overall range. Average adult home ranges (286 km²) were approximately 1% the size of the average foraging ranges of non-adults (10,540 km²–25,985 km²), with those of breeding adults being even smaller (95 km²). Home ranges of breeding adults did not vary in size between seasons but adults utilized their home range more intensively whilst breeding, moving greater distances during the incubation and chick hatching period. Range size and use increased as non-adults aged. Immatures and sub-adults had larger range sizes during winter, but range use of non-adults did not vary seasonally. Range size and use did not differ between the sexes in any of the age classes. Analyses of anthropogenic influences suggest that non-adults aged between 4-6 years face the greatest exposure to risk factors as a result of their larger range size and use, but also benefit by having better access to more feeding sites. Information on home range size and use and our approach to assessing age specific impacts of anthropogenic influences should enable more targeted management planning, education and conservation action in specific areas within the species' range.

Introduction

As human populations increase and service provision expands into previously undeveloped areas, many species which were previously shielded from anthropogenic influences are

exposed to the impacts of human development and their associated threats (Pimm *et al.* 1988, Fahrig 2007, Butchart *et al.* 2010). Mitigating any such threats requires a clear understanding of how species use their environment in both space and time, and such knowledge can play a critical role in designing effective conservation management strategies (Reed 1999, Clark *et al.* 2004, Serrano *et al.* 2008, Morrison and Wood 2009).

The spatial and temporal use of the environment may differ according to an individual's age, sex or breeding status and knowledge of these differences may further contribute to ensuring that management actions are targeted appropriately (González *et al.* 2006, Morrison and Wood 2009). This may be particularly important for species which take a long time to mature (Bennet and Owens 1997, Beissinger 2000, Penteriani and Delgado 2009). For example, large raptors often do not secure territories until they are several years old and their exploratory behaviour during this period may expose them to multiple threats across the wider landscape (Newton 1979, Mundy *et al.* 1992, Bamford *et al.* 2007, Phipps *et al.* 2013). Non-adult birds may therefore be exposed to different threats or different levels of threat than those found for adults (e.g. Ferrer 1993, Ferrer and Harte 1997, Penteriani *et al.* 2005a, Penteriani and Delgado 2009). In large raptors, non-adults form a large proportion of the population (Newton 1979, Brown *et al.* 1982, Kenward 2000), thus conservation measures designed to protect breeding birds only may not be sufficient to safeguard the population as a whole (Penteriani *et al.* 2005b, Gonzalez *et al.* 2006).

The Bearded Vulture *Gypaetus barbatus* is a large scavenging, sexually monomorphic (García *et al.* 2009) raptor that nests on high mountain cliffs in Africa, Europe and Asia and forages extensively over the surrounding mountains (Hiraldo *et al.* 1979, Brown 1997). Declines in Bearded Vulture populations have been documented throughout their range (Hiraldo *et al.* 1979, Del Hoyo *et al.* 1994, Frey 1996, Mingozi and Estève 1997, Acharya *et al.* 2010, Carrete *et al.* 2006, Margalida *et al.* 2008). In southern Africa the species is restricted to the Maloti-Drakensberg mountains of Lesotho and South Africa, where its range and population size have declined markedly in the last few decades and

there are now approximately 109 currently occupied territories (Brown 1991, Krüger *et al.* 2014, Chapter 2). This population is classified regionally as Critically Endangered as a result of these declines and the on-going threats faced by the population throughout its foraging range (Krüger *in press*).

A South African Biodiversity Management Plan, ratified by government, has been developed for the species (Krüger 2013). The primary objective of this plan is to halt the population decline in the short term. For the successful implementation of this plan, it is recognized that improved knowledge is required on how the species uses its environment. The size of the species' range in southern Africa and the political boundaries it encompasses make the planning, resourcing, coordinating, implementing and monitoring of conservation actions challenging. Therefore, detailed information on the spatial and temporal movements of Bearded Vulture, and knowledge of the risks/benefits associated with human activities within their range, will enable the prioritization of specific age classes or areas for focused action and the recommendation of suitable mitigatory measures for proposed developments.

The persistence of a threatened species relies on its breeding population and the protection of their breeding territories (Newton 1979, Bell and Merton 2002). In order to prioritize the breeding segment of the population for protection, information on breeding territory size is required. Previous studies have shown that breeding Bearded Vultures defend a territory around their nest site and that the size of their foraging range varies throughout the year (Brown 1988, Margalida and Bertran 2000, Bertran and Margalida 2002, Margalida and Bertran 2005). However, the core home range size for the southern African population remains unknown. Non-breeding birds on the other hand do not defend a territory and lead a nomadic lifestyle prior to breeding (Donázar 1993, Bertran and Margalida 2002, Urios *et al.* 2010). They are thought to inhabit more marginal areas within the species' range and therefore, in theory, may be exposed to a higher number and a wider range of threats which may negatively affect their survival prospects (Brown 1988).

Information on the ranging behaviour of Bearded Vulture in southern Africa is limited to five individuals tracked using conventional VHF radio-telemetry in the 1980s (Brown 1988) and a single juvenile tracked for less than 10 months using GPS satellite telemetry (Urios *et al.* 2010). This study therefore aims to provide a comprehensive understanding of the ranging behaviour of this population using a larger sample size across all age classes tracked with highly accurate GPS satellite technology which provides frequent and accurate locational data.

In addition to defining age-specific range size and use, understanding the extent of the exposure to risks or benefits within the foraging range can be useful in determining whether certain age classes are more vulnerable and therefore need to be targeted for conservation action. A number of risk assessment studies have focused on the vulnerability of raptor species to human-induced pressures such as recreation activities and developments (e.g. Kendall *et al.* 1996, Kenward 2006, Bamford *et al.* 2007, Carrete *et al.* 2012), although these have not necessarily discussed age specific threats.

Globally vultures are declining due to multiple threats including habitat loss, reduced food availability, poisoning, direct persecution, and fatal collisions with energy infrastructure (Virani *et al.* 2011, Ogada *et al.* 2012). The primary risks to the local population of Bearded Vultures are the use of poisons and the risk of collisions with energy structures (e.g. power lines and wind turbines) (Brown 1991, Mundy *et al.* 1992, Reid *et al. in review*, Rushworth and Krüger 2014). The abundance of these risk factors has increased over time due to rapid human population growth and development and their associated impacts (Statistics South Africa 2011, Virani *et al.* 2011, Ogada *et al.* 2012). In this chapter we consider the density of settlements, roads and power lines as a measure of negative human influence (*i.e.* types of risk). These factors result in habitat loss, land use change and the potential for persecution and poisoning. We considered feeding sites a positive human influence (*i.e.* type of benefit) which elevates the threat of food shortages and because numerous studies have shown supplementary feeding to benefit vulture populations (Bustamante 1996, Heredia and

Heredia 1999, Piper *et al.* 1999, Donázar *et al.* 2009, Cortés-Avizana *et al.* 2010), but see also Carrete *et al.* (2006), Oro *et al.* (2008) and Margalida (2010). We included the proportion of the foraging range that is formally protected as another beneficial human influence in our study because the benefits of protected areas in conserving species are well documented and numerous studies have found vulture populations to rely heavily on protected areas (e.g. Herremans and Herremans-Tonnoyer 2000, Thiollay 2006, Virani *et al.* 2011, Ogada *et al.* 2012). In addition, risks such as mass poisoning, persecution and collisions with electrical infrastructure are more prevalent in areas that are not formally protected (Mundy *et al.* 1992, Ogada *et al.* 2012).

We studied the movements of 18 Bearded Vultures in southern Africa between 2007 and 2014 and describe where (*i.e.* home range size), and how far (*i.e.* distances moved between points) individuals range and whether these parameters differ with age, sex and season/breeding status. Based on our findings on how Bearded Vultures utilize their environment, we delineate areas for the implementation of actions in the Biodiversity Management Plan for the species to guide conservation agencies in the effective use of resources. Additionally in this chapter we describe and compare exposure to potential risks and benefits to determine whether any particular age class is more exposed to anthropogenic influences as a result of their ranging behaviour and discuss the conservation implications of our findings. This approach may serve as a useful model for assessing exposure to risks for other endangered vulture species in Africa.

Methods

Capture and Marking

Eighteen Bearded Vultures were fitted with satellite Platform Transmitter Terminals (PTTs) between September 2007 and September 2012 in the Maloti-Drakensberg region of Lesotho and South Africa (Figure 4.1). Birds were caught at supplementary feeding sites (vulture

restaurants) using a noose carpet with pieces of meat, fat and bone as bait, and fitted with 70 g solar-powered GPS-PTT-100s (Microwave Telemetry Inc., Maryland, USA). The individuals were aged according to criteria in Brown (1989); juvenile (post-fledging to 2 years), immature (2-4 years), sub-adult (4-6 years) and adult (>6 years) (Figure 4.2). Juveniles, immatures and sub-adults are all classed as non-adults. Genetic sex determination was performed by Molecular Diagnostic Services (Pty Ltd., Westville, South Africa) using nucleic acid amplification procedures with blood taken from the brachial vein or from the tip of the feather shaft.

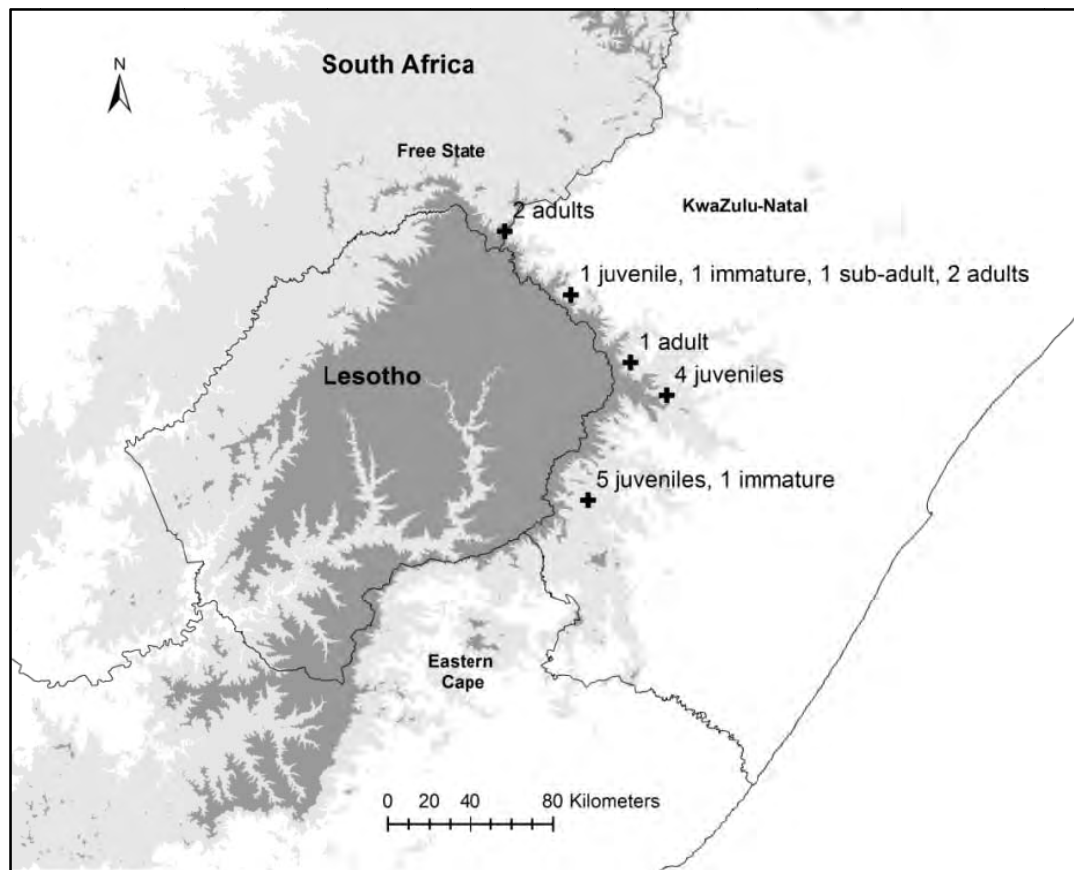


Figure 4.1 The location of the capture sites (+) within the Maloti-Drakensberg region in southern Africa, where the darker shades indicate higher altitudes; ■ dark grey= >2,000 m; ■ light grey= 1,600-2,000 m and white □= <1,600 m.



Figure 4.2 The four age classes of Bearded Vulture from Brown (1989); juvenile (post-fledging to 2 years), immature (2-4 years), sub-adult (4-6 years) and adult (>6 years).

In all cases, PTTs were attached using a pelvic harness attachment (Hegglin *et al.* 2004). The harnesses were constructed using a 2 mm silicon cord inserted into 0.25" tubular Teflon® which for added strength was then inserted into 0.33" tubular Teflon Ribbon® (Bally Ribbon Mills, Bally, Pennsylvania). The harnesses were constructed using a weak link sewn with dental floss initially (n=15), but after these proved too durable they were replaced by cotton thread (n=6) to allow birds to lose the harness after the end of the PTT's life cycle (Fuller 1987), predicted to be between five to eight years. The PTTs recorded one GPS position per hour from 05h00 to 20h00 hours (local time) daily as well as speed, date and time.

Ethics Statement

Vulture capture and marking procedures were approved by the Animal Ethics Committee of the Science Faculty of the University of Cape Town (reference: 2001\V14\SK), South African National Parks and Ezemvelo KwaZulu-Natal Wildlife (Research Project Registration number W/2057/01). Capture and handling of vultures and the fitting of tracking units were executed under the Endangered Wildlife Trust's Threatened or Protected Species registration certificate granted by the Gauteng Provincial Department of Agriculture, Conservation and Environment, South Africa (permit: 07046).

Spatial and Temporal Analyses

For all spatial analyses the GPS fixes were projected to the UTM coordinate system (WGS 1984 UTM Zone 35S) for use in R v.3.0.2 (R Core Development Team 2013), ArcGIS v.10.0 (ESRI, Redlands, USA) and the Geospatial Modelling Environment (GME) (Beyer 2012). For all temporal analyses we compared two seasons. For the non-adult age classes, our 'season' variable was either summer (1 October-31 March) or winter (1 April-30 September) whereas for adults, 'season' was either breeding (1 May-31 December) or non-breeding (1 January-30 April). We defined the breeding season as the period between courtship and nest building until fledging, and the non-breeding season as the post fledging period until natal dispersal upon initiation of nest building the following year (Brown 1990, *unpubl. data*). For all spatial analyses involving either monthly or seasonal comparisons, we used only data from individuals that were tracked for at least an entire month or an entire season respectively. Means are presented as mean \pm standard deviation throughout.

Home Range Size

The home range, utilization distribution, of each individual, was estimated by means of a kernel density approach (Kenward *et al.* 2001, Worton 1989, 1995). Total and monthly home range sizes were calculated in R using the package *adehabitatHR* v.0.4.10 (Calenge 2006) with the package *rgdal* v.0.8-16 (Bivand *et al.* 2013) to process the spatial data.

Home range estimates were derived by drawing contour lines (*i.e.* isopleths) based on the volume of the curve under the utilization distribution which defined home range polygons whose areas were then calculated. Fixed 90% and 50% kernel density contours were calculated to estimate the majority of the home range areas (90%), and the core (intensive use) areas (50%) (Fieberg 2007). A bivariate normal kernel was used which supposes that the utilization distribution is bivariate normal. Consequently the smoothing parameter was computed with the *ad hoc* method. The utilization distribution was estimated over a grid of a smaller size for adults (100 spatial pixels) than for non-adults (450 spatial pixels) because adult GPS fixes were concentrated in a much smaller area.

Additionally we merged the 50%, 75% and 90% kernel ranges of the three non-adult age classes to determine the geographical and administrative areas that were overlapped by each of these kernels for management planning purposes, *i.e.* the intensively used area (50% kernel) represents the minimum area for the implementation of conservation action.

We also calculated the overall foraging range of each individual as the Minimum Convex Polygon (MCP) encompassing all GPS fixes obtained for that individual (Worton 1989). Although MCPs have a tendency to overestimate the actual area occupied by the individual, they provide an indication of the overall foraging area and allow comparisons with historical studies.

Home Range Use

To quantify the extent of vulture movements, we determined the distance between hourly fixes for individuals across all age classes. Using GME, hourly flight distances were calculated as the straight-line distance between consecutive fixes that were separated by one hour within the same day, providing a minimum hourly distance travelled. For the analyses we used mean hourly distances per month for each individual.

Estimating Exposure to Risks and Benefits between Age Classes

The exposure to anthropogenic risks or benefits was described within each individual's 90% kernel home range using ArcGIS with shapefiles of the home ranges created in R using the *maptools* package (Bivand and Lewin-Koh 2013).

The following human influences (*i.e.* risk factors), which we thought to have a potential negative influence on age-specific survival, were considered: density of human settlements (number of houses per km²); density of power lines (sum of the lengths of 11, 22 and 132 kV lines in km per km²) and the density of roads (km of road per km²). These factors were considered risks since roads are the primary means of human access which influence patterns of settlement, create the potential for more poisoning and persecution activities, and result in land-use change which increases the likelihood of collisions with structures such as power lines. Collisions with power lines and poisoning are both known to have caused recent fatalities for the species (Smallie *et al.* 2009, Ogada 2014, Chapter 6). Other variables were considered as potential positive human influences (*i.e.* benefits) and were also compared between age classes; these included the percentage of formally protected land within a home range and the density of supplementary feeding sites (number per km²), plus the total number of supplementary feeding sites within a home range. Vulture populations have been found to rely heavily on protected areas (*e.g.* Herremans and Herremans-Tonnoyer 2000, Thiollay 2006, Virani *et al.* 2011, Ogada *et al.* 2012) and individuals are likely to be shielded

to a degree from threats in protected areas. Vultures have also been found to rely heavily on supplementary feeding (Bustamante 1996, Heredia and Heredia 1999, Donazar *et al.* 2009, Cortés-Avizana *et al.* 2010) and we consider these sites as beneficial in supplementing the food resource.

Statistical Analyses

See Appendix 4.1 for a summary of the analyses described below. We used the lme4 v.1.0-6 package (Bates *et al.* 2012) within R to perform Linear Mixed Models (LMM) with Wald chi-square tests to explore the relationships between age and i) home range size, and ii) hourly flight distances (*i.e.* home range use).

We calculated total range sizes and mean hourly distances travelled per month for each age class as described above. We then compared these between age classes and sexes by fitting age, sex and the interaction between them as fixed factors in the model (Appendix 4.1: I and II). The interaction between sex and age explored whether any difference in home range size or use between the sexes was consistent for each age class. Because duration of tracking may influence the accuracy of home range size, we included the log of the number of months each bird was tracked as a weighting term in the analyses comparing range size between age classes. In doing so we therefore attempted to account for the variable length of time for which we tracked different birds. Month and year were included as fixed factors in the home range use model to control for the effect of month or year on distances moved, because data were not fully balanced between these variables for each individual. Individual identity was included as a random term in these LMMs to account for the lack of independence between individuals in the different age classes because some birds crossed age classes as they aged. Pairwise comparisons between age classes and between the interaction terms were made using the lsmeans v.1.10-4 package (Lenth 2013) with *P* values adjusted using the Tukey method.

We then compared adult home range size and use between the breeding and non-breeding season using the home range size/use per breeding individual for each season as the response variable and fitting season and year as fixed factors in the model. Individual identity was again included as a random term because we had multiple years of data from some individuals. Some adults failed to breed ($n=2$) and the breeding season data from these non-breeding individuals were excluded for seasonal and monthly (see below) comparisons. We used this same model structure to examine temporal patterns of range size and use for non-adults (juveniles, immatures and sub-adults), but comparing the 'summer' and 'winter' seasons. For these seasonal analyses we grouped age classes where appropriate (see results).

To investigate temporal patterns of home range size and use by breeding adults throughout the year at a finer scale, we repeated these same models but with month, sex and year as fixed factors and monthly home range size per individual as the response variable. Although the sexes did not differ in total home range size (see results), we included sex as a factor in our monthly and seasonal comparisons, and the interaction between sex and month, and sex and season to explore whether breeding male and female home range sizes differed between months and seasons.

Risks and benefits within home ranges were compared across age classes using Generalized LMMs with age as a fixed factor and individual as a random term (Appendix 4.1: III). We analyzed the density of these variables by including their count (settlements or supplementary feeding sites) or length (roads or power lines) as the response variable and including the log of each individual's home range size as an offset in the model. These models were fitted with a Poisson distribution and log link function. For comparing access to supplementary feeding sites between ages, we analyzed the data using the total number of feeding sites in each individual's range with no offset. For examining the differences in the percentage of formally protected land in the range of each age class we analyzed the data using Arcsine square-root transformed percentages.

Results

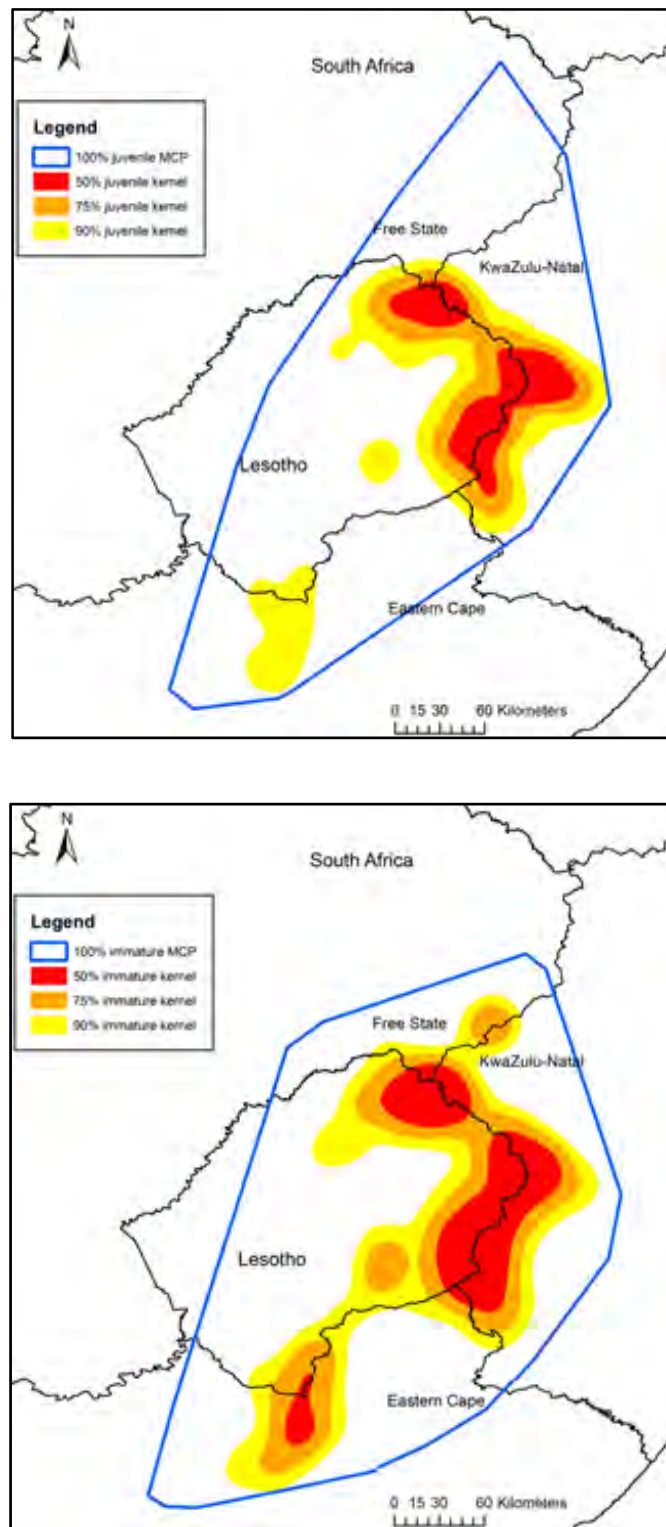
Home Range Size

We obtained satellite tracking data from 18 Bearded Vultures tracked for 392 bird-months (146,607 GPS fixes) between September 2007 and April 2014; 85 months of juvenile movements (22%), 113 months of immature movements (29%), 31 months of sub-adult movements (8%) and 163 months of adult movements (41%). For full details of each individual tracked see Appendix 4.2.

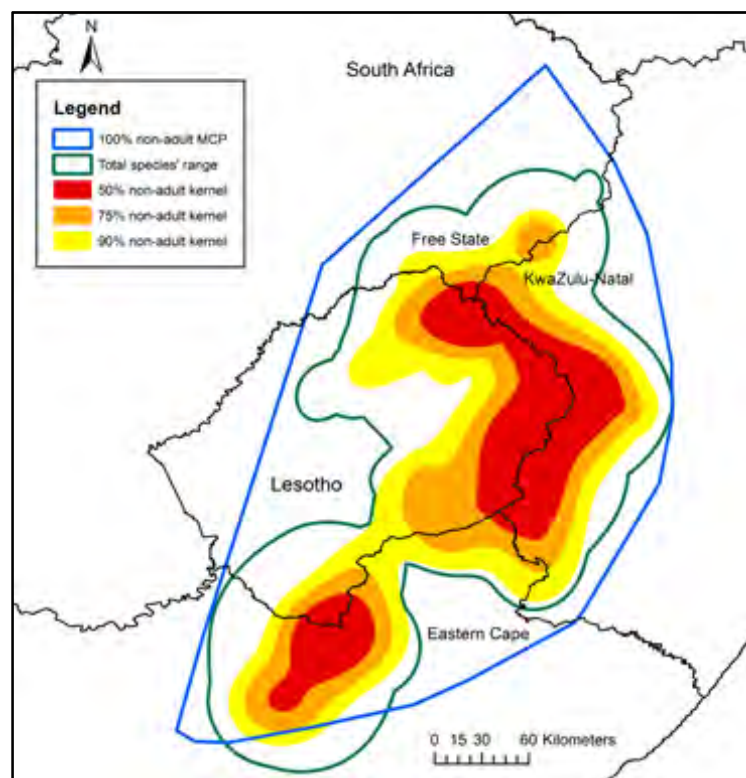
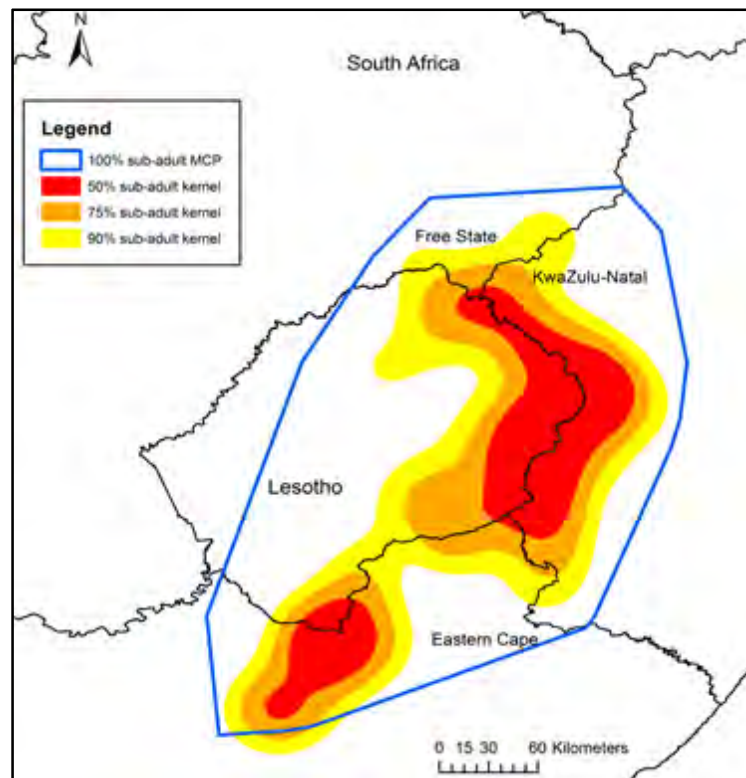
The total area of use of all age classes was 51,767 km² based on the 90% kernels of all individuals combined, and can be considered the species' foraging range. The foraging areas of non-breeding birds covered most of this area (Figures 4.3a-d) whereas adult home range areas were focused around their specific breeding territories with some overlap between territories (Figures 4.4a-d). The merged 50%, 75% and 90% kernels of non-adults, covered an area of 10,982 km², 21,454 km² and 33,636 km² respectively, of which the 90% kernel covered 65% of the population's foraging range (Figure 4.3d).

There was a significant difference in overall range size between age classes ($\chi^2_{(3)}=63.99$, $P<0.01$) with pairwise comparisons showing that the ranges of all age classes differed significantly in size ($P<0.01$) apart from immature and sub-adult ranges ($P=0.16$) (Figure 4.5). Non-adult range sizes increased as birds aged, prior to becoming adults but the home range size of adults, particularly breeding adults, was significantly smaller than those of all other age class (Table 4.1, Appendix 4.3). There was no significant difference in overall range size between sexes ($\chi^2_{(1)}=0.19$, $P=0.66$), although the interaction between age and sex was significant ($\chi^2_{(3)}=17.88$, $P<0.01$). Range sizes of males and females did not differ significantly within each age class but the difference in immature male ($17,254 \pm 2,155$ km²) and female ($26,802 \pm 2,184$ km²) range sizes was close to significant ($P=0.06$) and resulted in the significance of the interaction term. Home ranges estimated by MCPs showed a

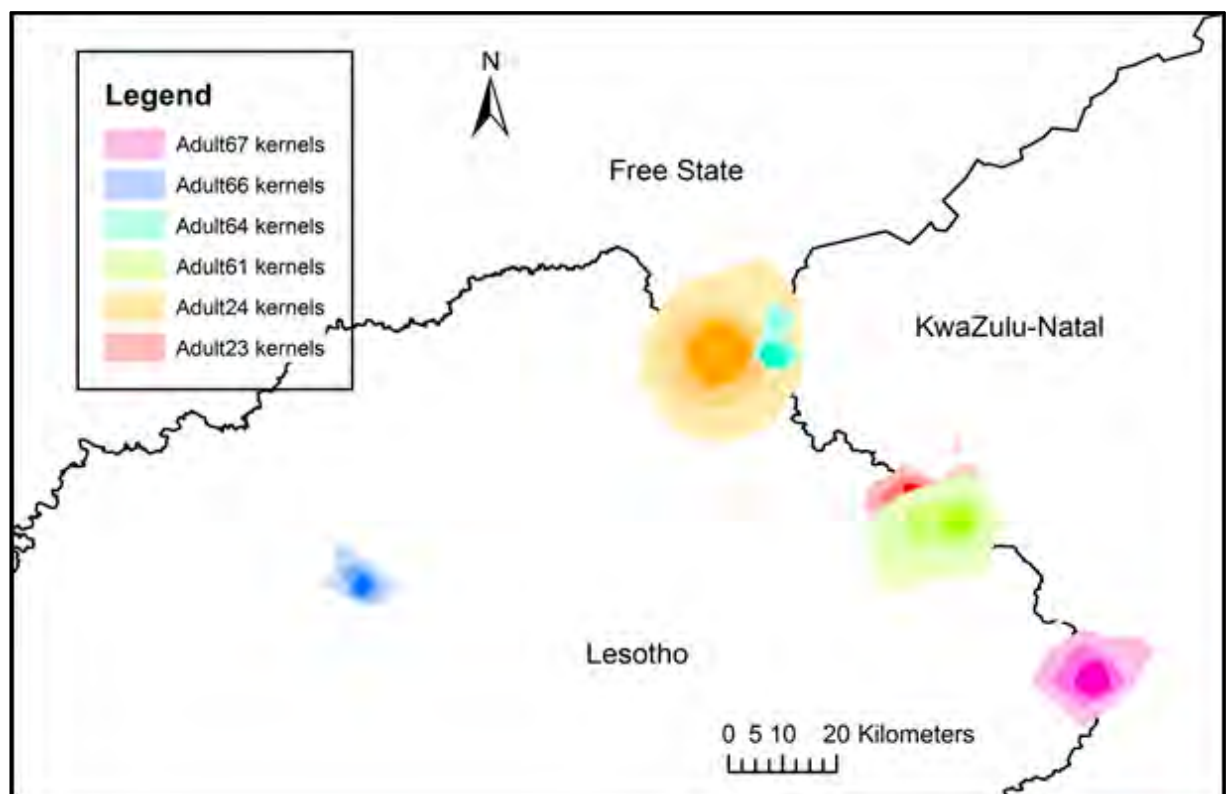
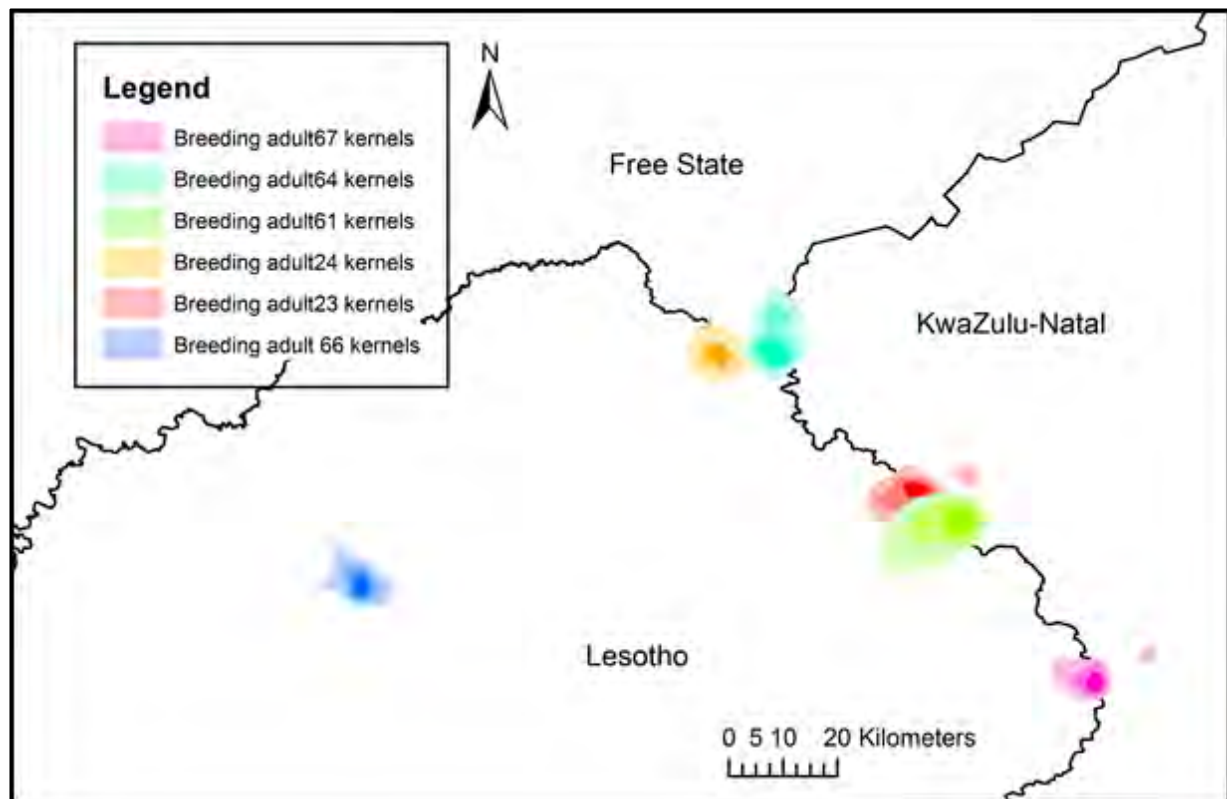
similar trend of increasing range size with age, although they were much larger overall (Figures 4.3a-d, Table 4.1).



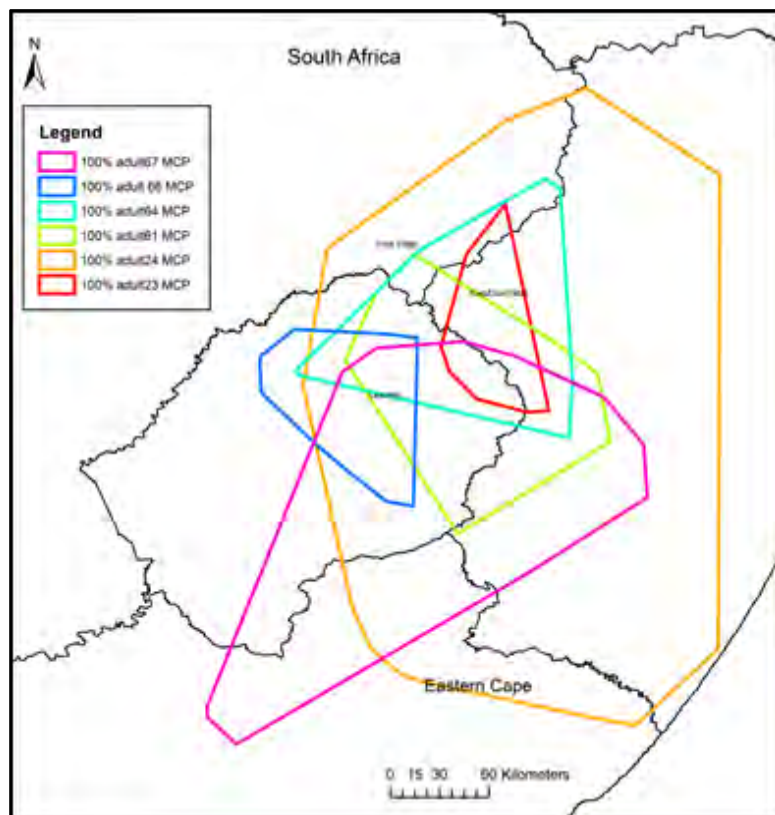
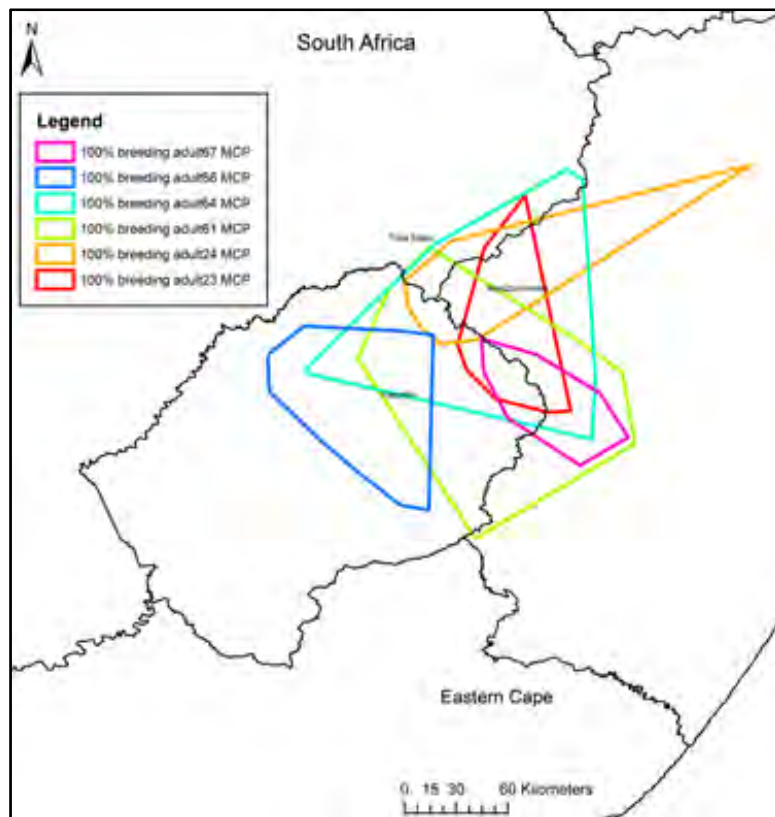
Figures 4.3 a&b. Bearded Vulture MCP and 50%, 75% and 90% kernel home ranges in southern Africa showing the total range collectively for a) juveniles (n=10) and b) immatures (n=7).



Figures 4.3 c&d. Bearded Vulture MCP and 50%, 75% and 90% kernel home ranges in southern Africa showing the total range collectively for c) sub-adults ($n=3$) and d) the merged ranges of non-adults ($n=20$) shown in relation to the overall range for the population indicating the geographic area in which to focus conservation action outside of protected areas.



Figures 4.4 a&b Bearded Vulture 50%, 75% and 90% kernel home ranges in southern Africa showing individual ranges for a) breeding adults (n=6) and b) all adults (n=6) including those they did not breed for a season (n=2), indicating some overlap of home ranges.



Figures 4.4 c&d Bearded Vulture MCP home ranges in southern Africa showing individual ranges for c) breeding adults (n=6) and d) all adults (n=6) including those they did not breed for a season (n=2), indicating some overlap of home ranges.

Table 4.1 A comparison of the total and seasonal 90% kernel home range estimates in km² (mean \pm standard deviation) and the Minimum Convex Polygon (MCP) home range estimates for different age classes of Bearded Vulture in southern Africa.

Age class	Total 90% kernel range size in km ²	Total MCP range size in km ²	Seasonal 90% kernel range in km ²	
			Non-breeding/ Summer	Breeding/ Winter
Juvenile	10,540 \pm 7,306	21,151 \pm 9,888	9,504 \pm 5,038	10,640 \pm 5,082
Immature	21,880 \pm 8,187	34,188 \pm 11,081	13,167 \pm 13,999	29,836 \pm 8,362
Sub-adult	25,985 \pm 7,077	40,961 \pm 9,274	27,272 \pm 11,005	33,573 \pm 8,497
Adult (total)	286 \pm 361	18,751 \pm 23,385	n/a	n/a
Adult (breeding)	95 \pm 19	5,220 \pm 3,850	105 \pm 62	148 \pm 108

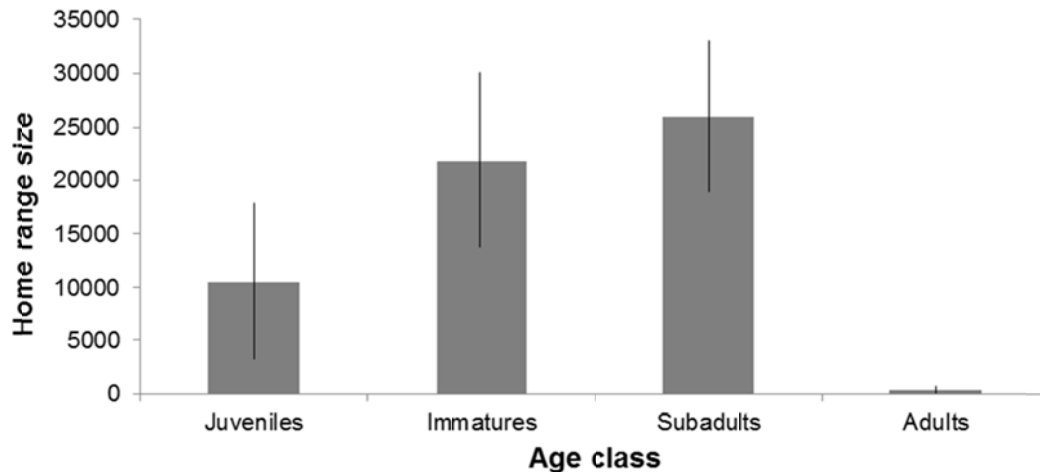


Figure 4.5 The average (mean \pm standard deviation) 90% kernel range size (in km²) of the different age classes showing an increase in range size with age for non-adults and a significantly smaller home range size for adults. Home range size differed between all age classes ($P < 0.001$) except between immatures and sub-adults ($P = 0.16$).

Adult home ranges did not differ significantly between the breeding (148 ± 62 km²) and non-breeding (105 ± 108 km²) seasons ($\chi^2_{(1)} = 3.21$, $P = 0.07$), nor did they differ between months

($\chi^2_{(1)}=0.67$, $P=0.41$). There were also no differences in monthly home range size between sexes ($\chi^2_{(1)}=0.01$, $P=0.94$). Since the total foraging ranges of immatures and sub-adults were similar (see above), these data were combined for seasonal analyses. Juvenile foraging ranges did not differ significantly seasonally ($\chi^2_{(1)}=2.84$, $P=0.09$) but foraging ranges of immature and sub-adults were on average significantly larger ($\chi^2_{(2)}=15.37$, $P<0.01$) during winter than in summer.

Home Range Use

Monthly mean hourly distances travelled varied significantly between age classes ($\chi^2_{(3)}=11.81$, $P<0.01$) but not between sexes within each age class ($\chi^2_{(1)}=0.26$, $P=0.61$). There was also no significant difference in the interaction between age and sex ($\chi^2_{(3)}=5.87$, $P=0.12$). Pairwise tests showed that the adults travelled significantly shorter distances than immatures ($P=0.03$) and sub-adults ($P=0.04$) but travelled similar distances to juveniles ($P=0.07$). Non-adult age classes did not differ significantly from each other in the mean distances travelled per month ($P>0.05$ in all cases) (Table 4.2), therefore these data were combined for further analyses. Range use reflected the general patterns of range size, with adults travelling the shortest distances and distances increasing in non-adults as they aged (Table 4.2, Appendix 4.3).

The movements of breeding adults varied significantly according to season ($\chi^2_{(1)}=34.89$, $P<0.001$) and month ($\chi^2_{(11)}=58.06$, $P<0.001$), with birds moving further between hourly fixes during the breeding season than the non-breeding season (Table 4.2) particularly during incubation and chick hatching (Figure 4.6). Sexes, however, did not differ in their movements either between seasons ($\chi^2_{(1)}=3.32$, $P=0.07$) or months ($\chi^2_{(1)}=0.02$, $P=0.89$) and there were also no significant interactions between sexes and seasons ($\chi^2_{(1)}=1.61$, $P=0.20$) and sexes and months ($\chi^2_{(1)}=7.98$, $P=0.71$). There were no significant seasonal differences in the movements of non-adults ($\chi^2_{(1)}=1.98$, $P=0.16$) (Table 4.2).

Table 4.2 A comparison of the average hourly distances (in km) between fixes (mean \pm standard deviation) of the different age classes of Bearded Vulture; sample sizes and ranges are also displayed. Pairwise comparisons of average distances indicated significant differences only between adults and immatures ($P=0.03$), and adults and sub-adults ($P=0.04$). Adult movements differed significantly between seasons ($P<0.001$) whereas non-adults did not ($P=0.16$).

Age class	Average hourly distance travelled	Non-breeding/ Summer	Breeding/ Winter
Juvenile	5.2 \pm 1.2 km (n= 7: 0-51 km)	5.0 \pm 1.2 km	5.5 \pm 1.2 km
Immature	6.8 \pm 1.6 km (n= 10: 0-123 km)	6.7 \pm 1.8 km	7.0 \pm 1.3 km
Sub-adult	7.8 \pm 1.8 km (n= 3: 0-109 km)	7.6 \pm 1.8 km	8.1 \pm 1.9 km
Adult	4.1 \pm 1.4 km (n= 6: 0-184 km)	3.2 \pm 0.8 km	4.4 \pm 1.5 km

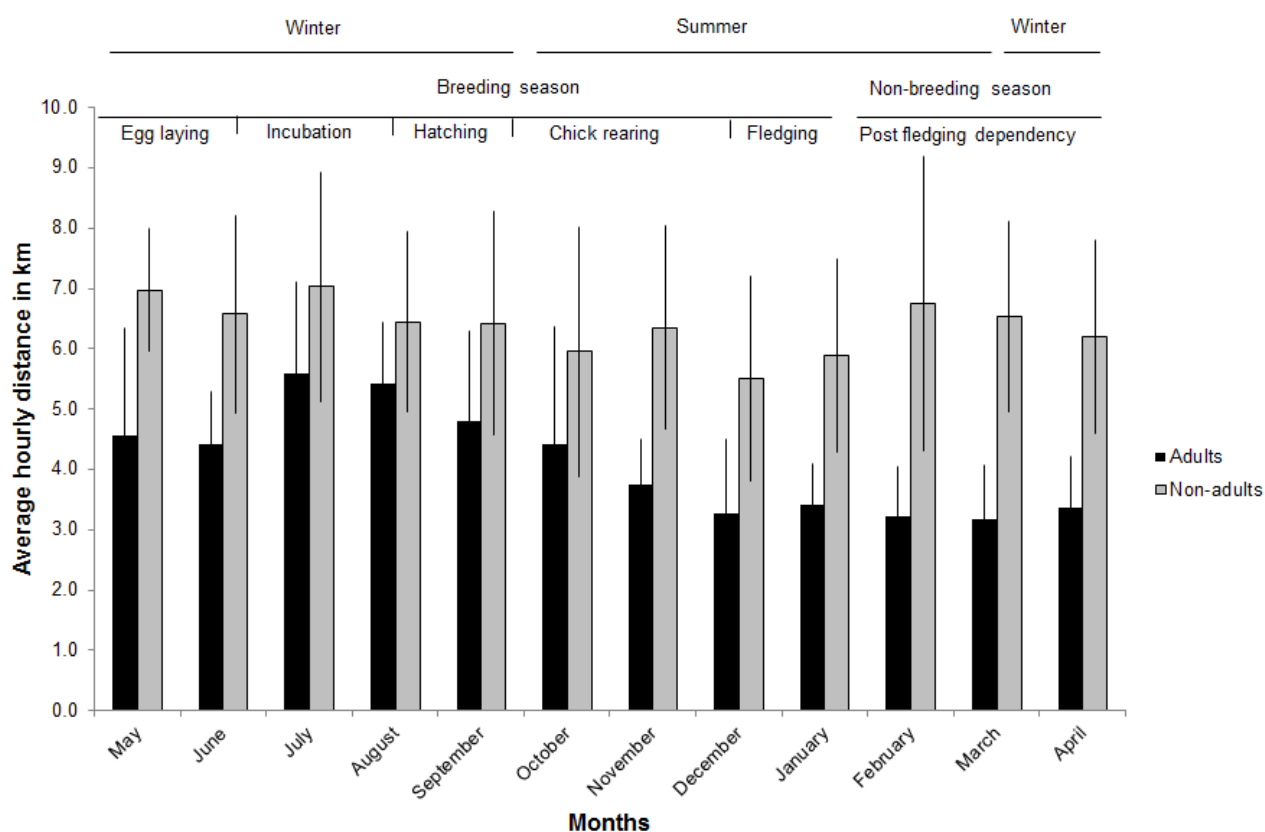


Figure 4.6 The mean (mean \pm standard deviation) monthly distances (in km) per hour between fixes of breeding adults, showing an increase in distances moved at the start of the breeding season in May, a peak during the incubation and hatching period and a decrease during the fledging period at the end of the breeding season (December) and during the post fledging period. The average (mean \pm standard deviation) monthly distances per hour (in km) of non-adults are shown for winter and summer.

Comparison of Exposure to Risks and Benefits between Age Classes

There were significant differences in the density of roads ($\chi^2_{(3)}=1,528.19$, $P<0.01$), power lines ($\chi^2_{(3)}=18,16.97$, $P<0.01$) and settlements ($\chi^2_{(3)}=66,746.89$, $P<0.01$) between age classes (Figure 4.7a). Pairwise comparisons showed that all age classes differed significantly in road ($P<0.01$), power line ($P<0.01$) and settlement ($P<0.05$) density within their home ranges, with only adults and juveniles having similar settlement densities in their range ($P=0.09$). Adults had the lowest exposure to these risk factors within their home range, whereas, sub-adults were the most exposed to these risks, having the highest density of settlements, power lines and roads in their range (Figure 4.7a).

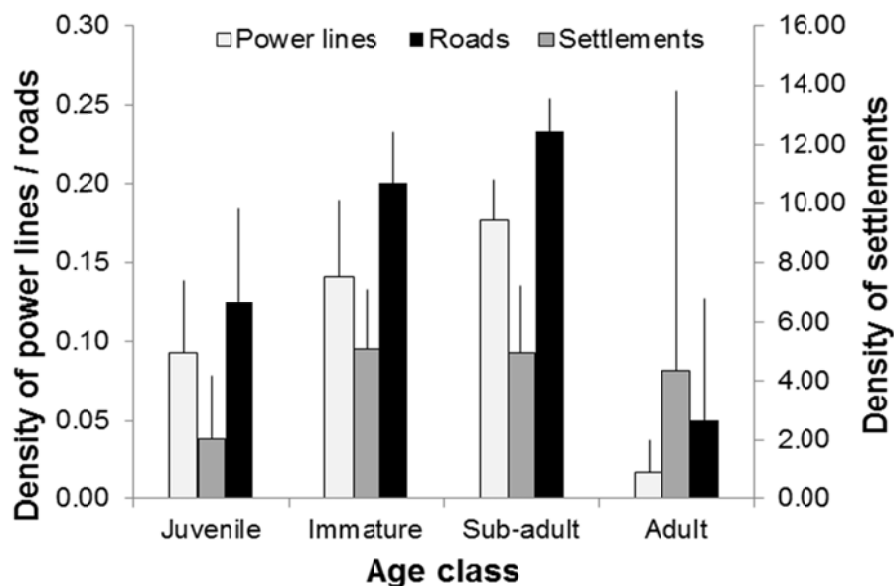


Figure 4.7a A comparison of the density (mean \pm standard deviation) of risk factors; power lines, roads and settlements per km² within the foraging range of different age classes of Bearded Vulture showing that immatures and subadults are exposed to a greater density of risks than juveniles and adults.

Age classes did not differ significantly in their exposure to two of the variables we defined as benefits; namely the density of feeding sites ($\chi^2_{(3)}=0.30$, $P=0.96$) and percentage of home range covered by protected areas ($\chi^2_{(3)}=1.76$, $P=0.62$). However, access to feeding sites, did differ significantly between ages ($\chi^2_{(3)}=68.31$, $P<0.01$). Pairwise comparisons indicated that

all age classes differed significantly ($P < 0.01$) in their access to feeding sites apart from sub-adults and immatures ($P = 0.09$) which had more feeding sites within their range than other age classes (Figure 4.7b). Even though a low percentage of their home range was protected, sub-adults in particular, had better access to feeding sites.

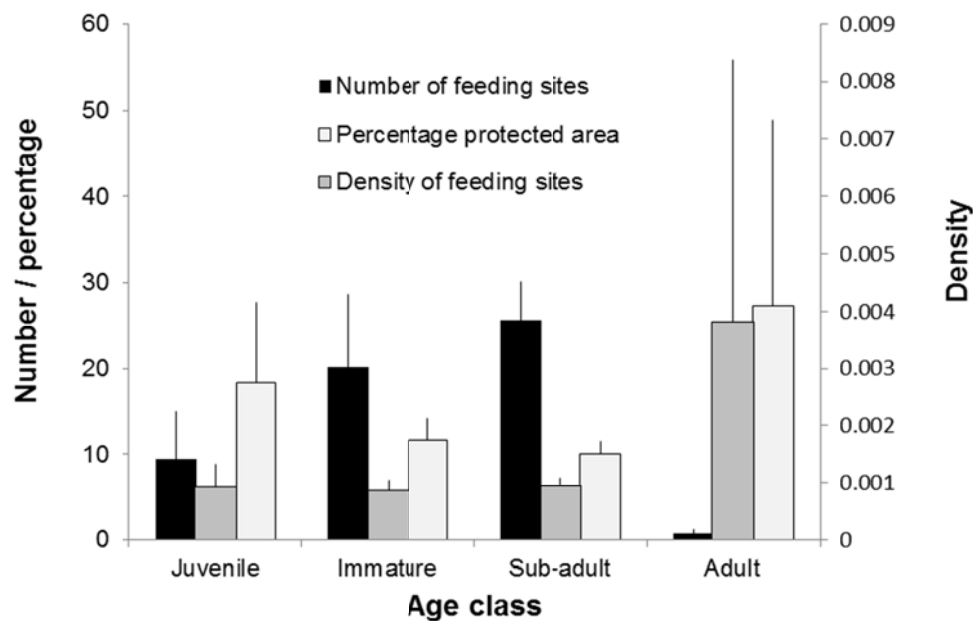


Figure 4.7b The average (mean \pm standard deviation) density and total number of feeding sites and the percentage of protected area within the foraging range of different age classes of Bearded Vulture. Although adults benefitted from a higher density of feeding sites and greater percentage of their home range protected, their access to feeding sites was not as high as for immatures and sub-adults.

Discussion

This study showed that the home range size of breeding adults was two orders of magnitude smaller compared to that of non-breeding adults which in turn were only 1% the size of non-adult ranges. The 90% kernel home range areas of all adults in this study (286 km²; 77-1000 km²) and those of only breeding adults (95 km²; 73-127 km²) were within the range of adult territory sizes in Europe (e.g. the Alps: 175 km², Hegglin *unpubl. data*; Pyrenees: 300 km², Terrasse *et al.* 1961 and the Caucasus: 206 km², Gavashelishvili and McGrady 2006). However, the MCP home ranges calculated for breeding adults in this study (5,220 km²;

2,726–12,343 km²) were 10 times larger than those estimated by Brown (1988) for the same population using radio telemetry (418 km²; 302–743 km²) and those home range areas calculated from inter-nest distances (625 km²; Brown *et al.* 1982) most probably because of the use of improved tracking technology. The average MCP home range area of juveniles in this study (21,151 km², n=12) was twice the size of reintroduced juveniles in the Alps (11,224 km², n=7) (Hegglin *unpubl. data*) and almost 10 times larger than those of juveniles in the Pyrenees (2,225 km², n=3) (Gil *et al. in press*). Our MCP calculations for non-adults (21,151–40,961 km²) were nearly identical to earlier findings of (Gil *et al.* 2010) for non-adults (23,683 km²–40,932 km²) within a similar sized distributional range in the Spanish-French Pyrenees but were larger than more recent estimates from the Pyrenees (945–19,008 km²) (Gil *et al. in press*). Again our estimates were much larger than the immatures tracked through conventional VHF radio telemetry by Brown (1988) which were described as having three areas of use, averaging 608 km² each (*i.e.* a total area of 1,825 km²). Our findings of increased range size and use with age in non-adults support the findings of Gil *et al.* (2010) and Margalida *et al.* (2013) who suggest that range size and use increases with age as the individuals explore their territory.

Although adults maintained the same home range size throughout the year, in contrast to the findings of Brown (1988) and Gil *et al.* (2010), their use of home range (based on minimum distances moved) was higher during the incubation and hatching/early chick rearing stages of the breeding cycle. Our findings suggest that breeding adults need to increase their search distances and intensity whilst breeding and spend less time on non-foraging related activities because of the need to return to the nest frequently. Incubation and chick rearing duties are shared by the sexes (Brown 1990), therefore the energy demand of both birds may be high after long periods of inactivity whilst incubating or guarding the chick. Winter is also a period of food shortage in the region because livestock are moved to lower altitudes and ungulate deaths are low at the beginning of the season thus birds may be required to fly further in search of food. Our theory of increased search

distances and intensity during incubating and chick hatching is supported by the tracking data, which on subsequent inspection showed that during these periods the birds spent only 22% of their time moving distances of less than 1 km per hour compared with 35% of the time in other months. In addition the frequency of movements greater than 10 km between fixes doubled during winter (13%) which is indicative of more extensive searching when food resources are scarce. The increased use of their home range during the breeding season makes breeding adults more vulnerable to risk factors during this period. Clearly the death of any adult through human influences during the breeding season would impact significantly on subsequent breeding performance.

Non-adults on the other hand increased the size of their range in winter but not the use of their range. The idea that the increased foraging range of immatures and sub-adults during winter may also be in response to food scarcity, is supported by the findings of Donazar (1993) who showed that variation in ranging behavior of non-adults was indicative of a spatially unpredictable or highly dispersed food resource. The movements may also be a response to interactions with conspecifics, territory exploration with age (immatures) and searching for a partner (sub-adults) (Bertran and Margalida 2002, Urios *et al.* 2010). The larger range sizes in winter and the greater distances moved by non-adults overall, makes them most vulnerable to risk factors such as illegal human activities and collisions with power lines throughout the year.

We found no differences between the sexes in either range size or use. This result is to be expected for a sexually monomorphic species (García *et al.* 2009) where parental duties are shared by adults (Brown 1990). Similarly Margalida *et al.* (2013) also found no dispersal differences between sexes in pre-adults and causes of mortality did not vary between sexes (Margalida *et al.* 2008).

The average home range size of adults in this study can help guide the size of the area (10 km radius) required to be conserved around each of the 109 breeding territories

identified in Chapter 2 for protection to safe-guard the breeding portion of the population. The radius of the core area (50% kernel) of use (4 km radius) represents the absolute minimum area for protection. The protection of the breeding territories will also benefit fledglings for the first few months before they disperse from their natal area. Similarly, the core area of the combined non-adult range (10,982 km²) also represents the minimum area to be conserved. However, since non-adult birds spread their activity over such large areas, the 75% (21,454 km²) and ideally the 90% kernels (33,636 km²) depict the areas in which resources for the implementation of actions need to be focused to effectively address the risks faced by non-adult birds. Preferred roost sites in these areas could form focal areas for conservation efforts and power lines and cables could be targeted for mitigation to reduce collision risks.

Our attempt at assessing the impacts of anthropogenic influences by age class provides useful information to identify the primary management actions required to reduce risks and maximize benefits in the priority areas. Apart from the protection of breeding territories, conservation management should also focus on the non-adult foraging range outside of protected areas. Since non-adult vultures range widely and do not necessarily benefit from protected areas (Phipps *et al.* 2013), our results suggest that efforts should concentrate on conservation actions within the wider range rather than the proclamation of additional protected areas, given the very small proportion of their foraging range that this would likely protect.

Sub-adults had larger ranges, moved greater distances and had a higher density of risk factors in their range than other age classes thus increasing their exposure to potentially lethal risk factors such as poisoning and power line collisions. Although we considered feeding sites beneficial through supplementation in times of food scarcity, they may also pose a risk, particularly to immatures and sub-adults that had better access to more feeding sites. Unintentional indirect poisoning through the use of veterinary drugs (Naidoo *et al.* 2009) or predator control measures (Krüger *et al.* 2006, Brown 1991, Virani *et al.* 2011,

Ogada *et al.* 2012), indirect persecution through traps placed at feeding sites for predator control (personal observation) and direct poisoning for the traditional medicine trade (Mander *et al.* 2007) are more likely to occur at feeding sites where scavengers are known to congregate frequently.

Further inspection of the tracking data suggests that non-adults do not rely heavily on supplementary feeding in contrast to the findings of Bustamante (1996), Heredia and Heredia (1999), Donázar *et al.* (2009) and Cortés-Avizana *et al.* (2010) and may not necessarily benefit from having access to more feeding sites. Less than 1% (0.62%; 0.03-1.49%) of the GPS fixes of immatures and sub-adults were within 1 km of a feeding site. Adults on the other hand used feeding sites significantly ($\chi^2_{(2)}=40.63$, $P<0.001$) more often (1.42%, 0-4.64%) with more than half (69%) of these fixes recorded during the breeding season. Breeding adults may therefore benefit from the provision of a consistent and regular supply of food close to their nest sites to reduce the need to range more extensively in the breeding season thus reducing risk and increasing breeding success. However, the potential negative impacts of feeding sites located in core breeding areas, such as a density-dependent decrease in productivity and changes in mating behaviour (Carrete *et al.* 2006, Oro *et al.* 2008, Margalida 2010), must be considered.

Furthermore, all age classes would benefit from improved management of existing sites since poisoning and persecution account for more than half the mortalities of the population (Chapter 6). The availability of supplementary food may influence recruitment by improving the survival rate of non-adult birds and should be investigated further. Additional actions to address poison use and persecution in the priority (core areas) include identifying alternative predator control methods and increasing awareness among commercial farmers and herders in communal areas. Emphasis must be on mitigation efforts during the breeding season to ensure breeding success is not compromised by human activities. In order to address the other risk factors, we recommend the mitigation or removal of unsafe energy structures and opposing or mitigating proposed infrastructural developments that will

encourage settlement in undeveloped areas and result in further habitat loss and land use change.

The larger sample size and the use of modern technology in this study have provided explicit information on the spatial and temporal movements of Bearded Vulture in southern Africa. This information should greatly aid conservation management planning for this species and should enable key requirements of the Biodiversity Management Plan for the species (Krüger 2013) to be addressed through assessing age specific exposure to anthropogenic influences. This is particularly important for the conservation of a species inhabiting an area spanning both international and regional boundaries in a landscape where human activities place vulture populations at risk in the long term. Although other raptor studies have looked at human influences, space use and conservation implications (e.g. Donazar *et al.* 2002, Bamford *et al.* 2007, Boshoff and Minnie 2011, García-Ripollés *et al.* 2011, Margalida *et al.* 2013, Boggie and Mannan 2014), these have often been limited because of their sample sizes or have they been focused on specific age classes, thus limiting the recommendations that can be made at the scale of the populations' foraging range.

We demonstrate that combining home range size and use estimates with simple indicators of the differential exposure to risk between age classes facilitates a more comprehensive understanding of how and where to address current and future threats to optimize conservation management strategies for a critically endangered population. This approach may be useful to assess risk exposure for other endangered vulture species in Africa that forage over extensive areas.

Acknowledgements

We are grateful to the capture team for their patience and tireless efforts; in particular Alfonso Godino, Allan Howell and Daniel Hegglin who were involved in the initial stages

(2007 and 2008), and Carmen Callero, Rickert van der Westhuizen and Ben Hoffman who assisted with the bulk of the captures from 2009 onwards.

We thank the following land owners/managers for their support and assistance with the monitoring, capture and marking activities; Peter Dommett, Henry Hibbett, Daryn Hiltunen, Brett Moller, Witsieshoek Mountain Resort staff, Ezemvelo KwaZulu-Natal Wildlife staff of the Maloti Drakensberg Park World Heritage Site and the South African National Parks staff of Golden Gate Highlands National Park.

The following institutions are thanks for providing data: The Lesotho Electricity Corporation, Eskom, South African Department of Transport, Maloti Drakensberg Transfrontier Programme and Ezemvelo KwaZulu-Natal Wildlife.

References

- Acharya R, Cuthbert R, Baral HS and Chaudhary A (2010) Rapid decline of the Bearded Vulture *Gypaetus barbatus* in Upper Mustang, Nepal. *Forktail* 26: 117-120.
- Bamford AJ, Diekman M, Monadjem A and Mendelsohn J (2007) Ranging behaviour of Cape Vultures *Gyps coprotheres* from an endangered population in Namibia. *Bird Conserv Int* 17: 331-339.
- Bates DM, Maechler M and Bolker B (2012) lme4: Linear mixed-effects models using Eigen and Eigenfaces. R package version 0.999999-0.
- Beissinger SR (2000) Ecological mechanisms of extinction. *Proc Natl Acad Sci USA* 97: 11688–11689.

- Bell BD and Merton DV (2002) Critically endangered bird populations and their management. In: Norris K. and Pain DJ (editors) *Conserving bird diversity. General principles and their application*. Cambridge University Press, Cambridge, pp. 105-138.
- Bennet PM and Owens IPF (1997) Variation in extinction risk among birds: chance or evolutionary predisposition? *Proc R Soc Lond B* 264: 401–408.
- Bertran J and Margalida A (2002) Territorial behaviour in Bearded Vultures in response to Griffon vultures. *J Field Ornith* 73: 86-90.
- Beyer HL (2012) Geospatial Modelling Environment (Version 0.7.2.0). (software). URL: <http://www.spatialecology.com/gme>.
- Bivand R, Keitt T and Rowlingson B (2013) rgdal: Bindings for the Geospatial Data Abstraction Library. R package version 0.8-10. <http://CRAN.R-project.org/package=rgdal>.
- Bivand R and Lewin-Koh N (2013) maptools: Tools for reading and handling spatial objects. R package version 0.8-24.
- Boggie MA and Mannan RW (2014) Examining seasonal patterns of space use to gauge how an accipiter responds to urbanization. *Landsc Urban Plan* 124: 34–42.
- Boshoff A and Minnie J (2011) On the role of the shape and size of foraging area, and colony size, in selecting critical areas for Cape Griffon *Gyps coprotheres* conservation action. *Vulture News* 61: 4-15.
- Brown CJ (1988) A study of the Bearded Vulture *Gypaetus barbatus* in southern Africa. Dissertation, University of Natal, Pietermaritzburg.
- Brown CJ (1989) Plumages and measurements of the bearded vulture in southern Africa. *Ostrich* 60: 165-171.

- Brown CJ (1990) Breeding biology of the Bearded Vulture in southern Africa, Parts I – III. *Ostrich* 61: 24-49.
- Brown CJ (1991) An investigation into the decline of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Biol Conserv* 57(3): 315-337.
- Brown CJ (1997) Population dynamics of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Afr J Ecol* 35(1): 53-63.
- Brown LH, Urban E and Newman K (1982) Birds of Africa Vol 1.:Academic Press, Orlando, Florida.
- Bustamante J (1996) Population viability analysis of Captive and Released Bearded Vulture Populations. *Conserv Biol* 10(3): 822-831.
- Butchart SHM *et al.* (2010) Global Biodiversity: Indicators of Recent Declines. *Science* 328(5982): 1164-1168. doi:10.1126/science.1187512.
- Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Modell* 197: 516-519.
- Carrete M, Donázar JA and Margalida A (2006) Density-dependent Productivity Depression in Pyrenean Bearded Vultures: Implications for Conservation. *Ecol Applic* 16(5): 1674–1682.
- Carrete M, Sánchez-Zapata JA, Benítez, JR, Lobón M, Montoya F and Donázar JA (2012) Mortality at wind-farms is positively related to large-scale distribution and aggregation in griffon vultures. *Biol Conserv* 145: 102–108.
- Clark RG, Hobson KA, Nichols JD and Bearhop S (2004) Avian Dispersal and Demography Scaling up to the Landscape and Beyond: *Condor* 106(4): 717-719.

- Cortez-Avazida A, Carrete M and Donázar JA (2010) Managing supplementary feeding for avian scavengers: guidelines for optimal design using ecological criteria. *Biol Conserv* 143: 1707-1715.
- Del Hoyo J, Elliott A and Sargatal J (1994) Handbook of the Birds of the World. Vol 2. Lynx Edicions, Barcelona.
- Donázar JA (1993) Los buitres ibéricos. Biología y conservación. J.M. Reyero, Madrid, Spain.
- Donázar JA, Blanco G, Hiraldo F, Soto-Largo E and Oria J (2002) Effects of forestry and other land use practices on the conservation of Cinerous Vultures. *Ecol Appl* 12: 1145-1456.
- Donázar JA, Margalida A, Carrete M and Sánchez-Zapata JA (2009) Too sanitary for vultures. *Science* 326(5953): 664.
- Fahrig L (2007) Non-optimal animal movement in human-altered landscapes. *Funct Ecol* 21: 1003–1015.
- Ferrer M (1993) Juvenile dispersal behaviour and natal philopatry of a long-lived raptor, the Spanish Imperial Eagle *Aquila adalberti*. *Ibis* 135: 132–138.
- Ferrer M and Harte M (1997) Habitat selection by immature Spanish Imperial Eagles during the dispersal period. *J Appl Ecol* 34: 1359–1364.
- Fieberg J (2007) Kernel density estimators of home-range: smoothing and the autocorrelation red herring. *Ecol* 88(4): 1059–1066.
- Frey H (1996) The situation of the Bearded Vulture (*Gypaetus barbatus*) in the Mediterranean countries. In: Muntaner J and Majol J (editors) Biología y Conservación de las Rapaces Mediterráneas, 1994. Monografías 4, SEO, Madrid.

- Fuller MR (1987) Application and considerations for wildlife telemetry. *J Raptor Res* 21: 126–128.
- García CB, Insausti JA, Gil JA, de Frutos A, Alcántara M, González J, Cortés MR, Bonafonte JI and Arruga MV (2009) Comparison of different procedures of DNA analysis for sex identification in the endangered bearded vulture (*Gypaetus barbatus*). *Eur J Wildl Res* 55(3): 309
- García-Ripollés C, López-López P and Urios V (2011) Ranging behaviour of non-breeding Eurasian Griffon Vultures *Gyps fulvus*: a GPS-telemetry study. *Acta Ornithol* 46(2): 127-134.
- Gavashelishvili A and McGrady MJ (2006) Breeding site selection by bearded vulture (*Gypaetus barbatus*) and Eurasian Griffon (*Gyps fulvus*) in the Caucasus. *Anim Conserv* 9: 159-170.
- Gil JA, Díez O, Báguena G, Lorente L, Pérez C, Losada JA and Alcántara M (2010) Juvenile dispersal of the bearded vulture (*Gypaetus barbatus*) in the Pyrenees (Spain-France). Fundación para la Conservación del Quebrantahuesos (FQC), Spain.
- Gil JA, Báguena G, Sánchez-Castilla E, Antor RJ, Alcantara M and López-López P (*in press*) Home-range and movements of non-breeding bearded vultures tracked by satellite telemetry in the Pyrenees.
- González LM, Arroyo BE, Margalida A, Sanchez R and Oria J (2006) Effect of human activities on the behaviour of breeding Spanish Imperial Eagles (*Aquila adalbertz*): management implications for the conservation of a threatened species. *Anim Conserv* 9: 85-93.
- Hegglin D, Wehrle M and Aebischer A (2004) Satellite tracking of Bearded Vultures - the project "Bearded Vultures on the Move". Annual Report of the Foundation for the conservation of the Bearded Vultures, pp. 52-55.

- Heredia R and Heredia B (1999) El Quebrantahuesos *Gypaetus barbatus* en los Pirineos: características ecológicas y biología de la conservación. The Bearded Vulture in the Pyrenees: ecology and conservation biology. Colección Técnica. ICONA, Madrid.
- Herremans M and Herremans-Tonnoyer D (2000) Land use and the conservation status of raptors in Botswana. *Biol Conserv* 94: 31–41.
- Hiraldo F, Delibes M and Calderon J (1979) El Quebrantahuesos: sistematica, taxonomia, biología, distrubucion y protección. Monografias 22, ICONA, Madrid.
- Kendall *et al.* (1996) An ecological risk assessment of lead shot exposure in non-waterfowl avian species: upland game birds and raptors. *Environ Toxicol Chem* 15(1): 4–20.
- Kenward R (2006) The goshawk. T. and A.D. Poyser, Ltd, London.
- Kenward RE, Walls SS, Hodder KH, Pahkala M, Freeman SN and Simpson VR (2000) The prevalence of non-breeders in raptor populations: evidence from rings, radio tags and transect surveys. *Oikos* 91: 271-279.
- Kenward RE, Clarke RT, Hodder KH and Walls SS (2001) Density and linkage estimators of home-range: nearest-neighbor clustering defines multi-nuclear cores. *Ecol* 82: 1905–1920.
- Krüger S (editor) (2013) Biodiversity Management Plan for the Bearded Vulture (*Gypaetus barbatus meridionalis*) for Southern Africa. Published 8 May 2014 Government Gazette Notice No 37620.
- Krüger S (*in press*) Bearded Vulture. In: Taylor MR (editor) The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. BirdLife, Johannesburg, South Africa.

- Krüger S, Piper S, Rushworth I, Botha A, Daly B, Allan D, Jenkins A, Burden D and Friedmann Y (editors) (2006) Bearded Vulture (*Gypaetus barbatus meridionalis*) Population and Habitat Viability Assessment Workshop Report. Conservation Breeding Specialist Group (SSC/IUCN)/CBSG Southern Africa, Endangered Wildlife Trust, Johannesburg.
- Krüger SC, Allan DG, Jenkins AR and Amar A (2014) Trends in territory occupancy, distribution and density of the Bearded Vulture *Gypaetus barbatus meridionalis* in southern Africa. *Bird Conserv Int* 24: 162-177. doi:10.1017/S0959270913000440.
- Lenth RV (2013) Using the lsmeans Package. The University of Iowa. Updated with lsmeans Version 1.10—July 4, 2013.
- Mander M, Diederichs N, Ntuli L, Khulile M, Williams V and McKean S (2007) Survey of the Trade in Vultures for the Traditional Health Industry in South Africa. Futureworks, *unpubl report*, 30 pp.
- Margalida A and Bertran J (2000) Breeding behaviour of the Bearded Vulture *Gypaetus barbatus*: minimal difference in parental activities. *Ibis* 142: 225-234
- Margalida A and Bertran J (2005) Territorial defence and agnostic behaviour of breeding bearded vultures *Gypaetus barbatus* towards conspecifics and heterospecifics. *Ethol Ecol Evol* 17: 51-63.
- Margalida A, Heredia R, Razin M and Hernandez M (2008) Sources of variation in mortality of the Bearded Vulture *Gypaetus barbatus* in Europe. *Bird Conserv Int* 18: 1-10.
- Margalida A (2010) Supplementary feeding during the chick-rearing period is ineffective in increasing the breeding success in the bearded vulture (*Gypaetus barbatus*). *Eur J Wildl Res* 56: 673–678.

- Margalida A, Carrete M, Hegglin D, Serrano D, Arenas R and Donázar JA (2013) Uneven Large-Scale Movement Patterns in Wild and Reintroduced Pre-Adult Bearded Vultures: Conservation Implications. *PLoS ONE* 8(6): e65857. doi:10.1371/journal.pone.0065857.
- Mingozzi T and Estève R (1997) Analysis of a historical extirpation of the Bearded vulture *Gypaetus barbatus* (L.) in the Western Alps (France-Italy): former distribution and causes of extirpation. *Biol Conserv* 79: 155-171.
- Morrison JL and Wood PB (2009) Broadening our approaches to studying dispersal in raptors. *J Raptor Res* 43(2): 81-89.
- Mundy P, Butchart D, Ledger J and Piper S (1992) The Vultures of Africa. Russel Friedman Books cc, Johannesburg, South Africa.
- Naidoo V, Wolter K, Cuthbert R and Duncan N (2009) Veterinary diclofenac threatens Africa's endangered vulture species. *Reg Toxicol Pharmacol* 53: 205–208.
- Newton I (1979) Population ecology of raptors. T and AD Poyser, Berkhamsted.
- Ogada DL (2014) The power of poison: pesticide poisoning of Africa's Wildlife. *Ann NY Acad Sci*. doi: 10.1111/nyas.12405.
- Ogada DL, Keesing F and Virani MZ (2012) Dropping dead: causes and consequences of vulture population declines worldwide. *Ann NY Acad Sci* 1249: 57-71.
- Oro D, Margalida A, Carrete M, Heredia R and Donázar JA (2008) Testing the Goodness of Supplementary Feeding to Enhance Population Viability in an Endangered Vulture. *PLoS ONE* 3(9): e4084. doi:10.1371/journal.pone.0004084.
- Penteriani V and Delgado MM (2009) Thoughts on Natal Dispersal *J Raptor Res* 43(2): 90-98.

- Penteriani V, Otalor F and Ferrer M (2005) Floater survival affects population persistence. The role of prey availability and environmental stochasticity. *Oikos* 108: 523-534.
- Penteriani V, Otalora F, Sergio F and Ferrer M (2005) Environmental stochasticity in dispersal areas can explain the 'mysterious' disappearance of breeding populations. *Proc R Soc B* 272: 1265-1269. doi:10.1098/rspb.2005.3075.
- Phipps WL, Willis SG, Wolter K and Naidoo V (2013) Foraging Ranges of Immature African White-Backed Vultures (*Gyps africanus*) and Their Use of Protected Areas in Southern Africa. *PLoS ONE* 8(1): e52813. doi:10.1371/journal.pone.0052813.
- Pimm SL, Jones HL and Diamond J (1988) On the risk of extinction. *Am Nat* 132: 757-785.
- Piper SE, Boshoff AF and Scott HA (1999) Modelling survival rates in the Cape Griffon *Gyps coprotheres*, with emphasis on the effects of supplementary feeding. *Bird Study* 46: 230–238.
- R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org>.
- Reed JM (1999) The role of behavior in recent avian extinctions and endangerments. *Conserv Biol* 13: 232-241.
- Reid T, Krüger S, Whitfield P and Amar A (*in review*) Spatial analyses of Bearded Vulture movements in southern Africa to inform wind turbine placement.
- Rushworth I and Krüger S (2014) Wind farms threaten southern Africa's cliff-nesting vultures. *Ostrich* 85(1): 13-23. doi:10.2989/00306525.2014.913211.
- Serrano D, Carrete M and Tella J (2008) Describing dispersal under habitat constraints: a randomization approach in Lesser Kestrels. *Basic Appl Ecol* 9: 771-778.

- Smallie J, Diamond M and Jenkins A (2009) Lighting up the African continent – what does it mean for our birds? In: Harebottle DM, Craig AJFK, Anderson MD, Rakotomanana H and Muchai (editors) Proc 12th Pan-Afr Ornithol Cong, 2008. ADU Cape Town, pp. 38–43.
- Statistics South Africa (2011) Mid-year population estimates 2011. Pretoria, South Africa: Statistical release, P0302.
- Terrasse JF, Terrasse M and Boudoint Y (1961) Observations sur la reproductions du vautour fauve, du percnoptère et du gypaete barbu dans les Basses-Pyrénées. *Alauda* 29: 1-24.
- Thiollay J (2006) Severe decline of large birds in the Northern Sahel of West Africa: a long-term assessment. *Bird Conserv Int* 16: 353–365.
- Virani MZ, Kendall C, Njoroge P and Thomsett S (2011) Major declines in the abundance of vultures and other scavenging raptors in and around the Masai Mara ecosystem, Kenya. *Biol Conserv* 144: 746-752.
- Urios V, López-López P, Limiñana R and Godino A (2010) Ranging behaviour of a juvenile Bearded Vulture (*Gypaetus barbatus meridionalis*) in South Africa revealed by GPS satellite telemetry. *Ornis Fenn* 87: 1-5.
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecol* 70: 164-168.
- Worton BJ (1995) Using Monte Carlo simulation to evaluate kernel-based home-range estimators. *J Wildl Manage* 59: 794-800.

Appendices

Appendix 4.1 The three key analyses with a description of the analytical approach used, specifying the response and explanatory terms (fixed and random terms) included in models.

Analytical approach		
I. Comparing home range sizes between individuals (Linear Mixed Models)		
Analysis	Response	Explanatory variable (random terms in parentheses): Distribution
1a) Influence of age class and sex on total home range size	Total 90% kernel home ranges	Age, Sex, Age*Sex, (Individual): Normal, log (number of months of data)
1b) Influence of season on home range of breeding adults	90% kernel home ranges by season	Season, Year, (Individual): Normal
1c) Influence of month on home range of breeding adults	90% kernel home ranges by month	Sex, Month, Year, (Individual): Normal
1d) Influence of season on home range of juveniles	90% kernel home ranges by season	Season, Year, (Individual): Normal
1e) Influence of season on home range of immatures and sub-adults	90% kernel home range by season	Season, Year, (Individual): Normal
II. Comparing hourly distances moved between individuals (Linear Mixed Models)		
Analysis	Response	Explanatory variable (random terms in parentheses): Distribution
2a) Influence of age class and sex on average hourly distances	Average hourly distance	Age, Sex, Age*Sex, Month, Year, (Individual): Normal
2b) Influence of season on distance of breeding adults	Average hourly distance by season per year	Sex, Season, Sex*Season, Year, (Individual): Normal
2c) Influence of month on distance of breeding adult	Average hourly distance by month per year	Sex, Month, Sex*Month, Year, (Individual): Normal
2d) Influence of season on distance of non-adults	Average hourly distance by season per year	Season, Year, (Individual): Normal
III. Comparing risk and benefit factors (Generalized Linear Mixed Models)		
Analysis	Response	Explanatory variable (random terms in parentheses): Distribution (link/offset)
3a) Settlements	Total number of settlements	Age, (Individual): Poisson (log/90% kernel range)
3b) Roads	Total km of roads	Age, (Individual): Poisson (log/90% kernel range)
3c) Power lines	Total km of power lines	Age, (Individual): Poisson (log/90% kernel range)
3d) Feeding site access	Total number of feeding sites	Age, (Individual) : Poisson (log/none)
3e) Feeding site density	Number of feeding sites per km ²	Age, (Individual): Poisson (log/90% kernel range)
3f) Proportion of protected area	Percentage of protected area	Age, (Individual): Arcsine square-root (percentage protected)

Appendix 4.2 Details of the 18 Bearded Vultures caught in southern Africa and the tracking information used for analyses between September 2007 and April 2014.

Age class	Individual	Sex	Transmission date († end date as a result of death of bird)		Number of tracking months	Number of GPS fixes
			Start	End		
Juvenile	49182	Female	2007/09/06	2008/05/27†	8	1,724
	19853	Male	2009/08/08	2010/08/31	12	3,539
	93462	Male	2009/08/20	2010/08/31	12	4,061
	93463	Female	2009/08/26	2010/08/31	12	4,879
	93465	Female	2010/07/06	2011/08/31	13	4,537
	93468	Female	2009/08/12	2010/08/31	12	4,200
	108925	Female	2012/07/29	2012/12/31	4	2,042
	108926	Male	2012/09/02	2012/12/31	4	1,592
	108927	Male	2012/09/03	2012/12/31	4	1,651
	108928	Male	2012/09/17	2012/12/31	4	1,223
Immature	19853	Male	2010/09/01	2012/08/31	24	6,351
	93462	Male	2010/09/01	2012/08/31	24	8,052
	93463	Female	2010/09/01	2012/08/31	24	8,461
	93465	Female	2011/09/01	2012/10/15†	13	4,543
	93468	Female	2010/09/01	2012/04/01†	19	6,473
	93461(1)	Female	2009/08/23	2010/05/08	8	2,920
	93464(1)	Male	2010/07/06	2010/08/30†	1	340
Sub-adult	19853	Male	2012/09/01	2013/03/31	7	1,825
	93462	Male	2012/09/01	2013/08/31	12	3,446
	93463	Female	2012/09/01	2013/08/31	12	3,880
Adult	93461(2)	Female	2010/08/10	2012/12/31	28	16,420
	93464(2)	Female	2011/09/11	2014/04/30	31	9,651
	93467	Female	2010/07/21	2012/08/10†	24	12,821
	93466	Female	2010/09/01	2014/04/30	44	18,185
	108923	Male	2012/08/16	2013/12/31†	16	7,356
	108924	Male	2012/08/26	2014/04/30	20	6,435
Total	26	14F, 12M	-	-	392	146,607

Appendix 4.3 Bearded Vulture ranging information showing average hourly flight distances and kernel and MCP home range sizes in km² depicted by individual separated by age class.

Age	Individual	Sex	Average hourly flight distance (mean \pm standard deviation)	Kernel home-range		MCP home-range
				90%	50%	
Juvenile	49182	female	6.5 \pm 1.8 (0-43.1)	27,288	6,006	33,504
	19853	male	5.6 \pm 0.9 (0-42.2)	9,021	2,759	17,564
	93462	male	5.9 \pm 0.8 (0-42.8)	15,386	3,814	31,205
	93463	female	4.3 \pm 0.9 (0-41.6)	6,142	1,420	18,529
	93465	female	5.0 \pm 0.9 (0-51.1)	16,739	4,015	32,606
	93468	female	5.3 \pm 1.1 (0-47.1)	9,222	2,514	16,166
	108925	female	4.8 \pm 0.5 (0-38.5)	6,862	1,687	13,654
	108926	male	4.9 \pm 0.6 (0-40.4)	6,895	1,766	17,462
	108927	male	3.7 \pm 0.7 (0-47.1)	3,515	1,121	5,565
	108928	male	4.3 \pm 0.9 (0-38.7)	4,334	1,394	7,755
Immature	19853	male	6.3 \pm 1.4 (0-52.1)	25,145	7,028	48,013
	93461(1)	female	9.4 \pm 1.7 (0-52)	36,204	11,660	47,818
	93462	male	6.9 \pm 1.2 (0-60.5)	23,793	6,166	46,278
	93463	female	6.6 \pm 1.7 (0-123)	10,789	2,542	26,368
	93464(1)	male	8.5 \pm - (0-42.8)	18,808	5,090	20,263
	93465	female	7.2 \pm 1.0 (0-61.7)	23,449	6,689	35,546
	93468	female	6.2 \pm 1.4 (0-85.4)	14,971	3,210	34,570
Sub-adult	19853	male	7.8 \pm 1.8 (0-49.2)	22,690	6,086	34,741
	93462	male	8.5 \pm 1.9 (0-109)	34,109	10,088	51,620
	93463	female	7.0 \pm 1.6 (0-56.8)	21,157	6,785	36,521
Adult	93461(2)	female	4.4 \pm 1.8 (0-62.8)	127	29	12,343
	93464(2)	female	4.5 \pm 1.4 (0-81.5)	99	15	1,948
	93466	female	3.3 \pm 0.9 (0- 24.3)	77	11	5,680
	93467	female	3.8 \pm 0.9 (0-56.7)	315	63	27,245
	108923	male	3.7 \pm 5.3 (0-89.9)	95	14	2,798
	108924	male	4.0 \pm 0.8 (0-183.8)	1,000	149	62,494

Chapter 5: Genetic structure in the Bearded Vulture *Gypaetus barbatus*: reduced diversity in southern Africa



Photo 5 Adult Bearded Vulture from the sub-species *G. barbatus meridionalis* (left) lacking the black ear tuft that distinguishes it from *G. barbatus barbatus* (right)

A modified form of this chapter is published in Ibis:

Krüger SC, Wesche PL and Jansen van Vuuren B (2014) Reduced genetic diversity in Bearded Vultures *Gypaetus barbatus* in Southern Africa. doi: 10.1111/ibi.12200.

Abstract

The Bearded Vulture *Gypaetus barbatus* occurs globally as small and dwindling population fragments with limited genetic differentiation amongst populations, suggesting that the species might globally be managed as a single entity. Given that the numbers of East and southern African Bearded Vultures included in previous studies were small, our aim here is to determine the genetic variation within, evolutionary placement of, and connectivity amongst sub-Saharan African populations. Mitochondrial DNA fragment analyses detected little to no differentiation between populations in Ethiopia and southern Africa, with reduced haplotype diversity in southern Africa compared with populations in the Northern Hemisphere. Our results directly inform conservation management of this species globally and locally, and provide guidelines for translocations should populations continue to decline.

Introduction

Many natural populations are becoming increasingly fragmented as a result of anthropogenic influences. Fragmentation negatively affects population viability through loss of genetic diversity, inbreeding, and ultimately population growth and adaptability (see *e.g.* Lowe *et al.* 2005 and references therein). A case in point concerns the Bearded Vulture *Gypaetus barbatus*, a large scavenging raptor inhabiting mountainous areas across an extensive range. In the past, the species was widely distributed throughout much of Asia, Europe and Africa, however, its current distribution is severely fragmented. Although the species never occurred in high numbers, trends of recent decline throughout much of its range have been documented (Margalida *et al.* 2008, Birdlife International 2014, Krüger *et al.* 2014, Chapter 2).

Two distinct subspecies were recognized based on plumage characteristics (Hiraldo *et al.* 1984, Mundy *et al.* 1992). *G. b. barbatus* occurs north of the Tropic of Cancer while *G. b. meridionalis* was described from south of the Tropic of Cancer. The sub-Saharan African

(*G. b. meridionalis*) birds have similar phenotypes in that they lack a black 'ear' tuft and breast collar and are smaller in size compared with their northern counterparts. Whilst a genetic study by Godoy *et al.* (2004) confirmed the presence of two lineages, these had little geographic correspondence to the described subspecies. The first lineage occurs mainly in Western Europe while the second is found predominantly in Africa, Eastern Europe and Central Asia. These findings led to the suggestion by Godoy and co-workers that the species should be managed as a single population. Only a few sub-Saharan African, and specifically southern African, samples were included in the Godoy *et al.* (2004) study. For this reason, the evolutionary position of the southern (and to a lesser extent East) African populations, and the level of connectivity (migrant exchange) between them, remains unclear.

Following recent assessments, African Bearded Vulture populations are in decline or presumed to be declining. Ash and Atkins (2009) suspected that the Ethiopian population was much smaller than the crude estimate by Mundy *et al.* (1992) of 1,430 pairs. Populations in Kenya, Tanzania and Uganda are estimated at only 10 pairs (S. Thomsett *pers. comm.*) whilst the southern African population is estimated at 109 pairs (Krüger *et al.* 2014, Chapter 2). The latter also suffered a significant range contraction (Boshoff *et al.* 1983, Krüger *et al.* 2014, Chapter 2).

For the long-term persistence of the Bearded Vulture in southern Africa it is essential to maintain an adequate population size and high levels of genetic diversity. If there is some exchange of individuals between sub-Saharan populations, genetic diversity in populations could benefit. We therefore aim to extend the Godoy *et al.* (2004) study through increasing the southern and East African (specifically Ethiopian) sample sizes. Knowledge regarding the exact evolutionary placement of southern and East African populations, and suggestions regarding connectivity among populations, will contribute information towards the management of Bearded Vultures locally as well as globally.

Methods

Samples

Blood, tissue or feather samples for DNA analyses were collected from 40 individuals between 2000-2012 (details provided in Appendix 5.1). Only one feather was collected at each site to avoid possible duplication of samples from a single specimen.

DNA Isolation, Polymerase Chain Reaction (PCR) and Sequencing

DNA was extracted using a commercial DNA extraction kit (DNeasy Blood and Tissue kit; Qiagen, Hilden, Germany). As our study follows on from the work of Godoy and co-workers, we followed their laboratory protocols, including PCR parameters, to ensure comparable data. Amplification was performed using the control region primers QHD-2F and Fbox-2R. Eleven individuals (Appendix 5.1), including representatives of each haplotype identified by the control region data were, subsequently sequenced for cytochrome b using primers L14841 (Kocher *et al.* 1989) and H15915 (Irwin *et al.* 1991). Sequencing was performed with BigDye[®] Terminator 3.1 mix (Applied Biosystems, Warrington, United Kingdom). Purified sequencing products were run on an Applied Biosystems 3130 xl Genetic Analyzer. Sequences were edited using Genious R6 (Biomatters, available from www.geneious.com).

Analyses

Data generated in this study were aligned with those published by Godoy *et al.* (2004) using ClustalW (Larkin *et al.* 2007) within MEGA 6 (Tamura *et al.* 2013). Analyses were based on 40 samples comprising 216 base pairs. The Oriental White-backed Vulture *Gyps bengalensis* was included as an outgroup (GenBank accession number EU752279, Johnson *et al.* 2008).

As is appropriate for closely related haplotypes, we constructed a haplotype network in TCS (Clement *et al.* 2000). We had to introduce a two base pair indel to ensure optimal alignment, and followed Joly *et al.* (2007) in handling missing data. To support the network analyses, we constructed phylogenetic trees in MEGA 6 under a maximum likelihood approach. The evolutionary model that best fitted our data (the Kimura 2- parameter model, gamma distributed with invariant sites) was determined on the basis of the Bayesian Information Criterion (BIC) using MEGA 6. Nodal support was determined through 10,000 bootstrap replicates. To determine whether genetic diversity in the southern African/Ethiopian samples is geographically structured, an Analysis of Molecular Variance (AMOVA) was performed in Arlequin 3.5 (Excoffier *et al.* 2005). For this, we performed two analyses; one in which we specified all populations as a single group and a second in which we considered the Ethiopian samples separate from the southern African samples.

To assess genetic variation within the southern African region, we selected samples from Godoy *et al.* (2004) as a reference group. We specifically looked for an area with similar geographic coverage and positioning (edge of the range) and high sampling density. The Iberian Peninsula (n=61 specimens) matched these selection criteria. We then sub-sampled Godoy *et al.*'s (2004) Iberian haplotypes through 100,000 bootstrap iterations to compare with the number of haplotypes recovered from the 37 southern African samples.

Results

Three polymorphic sites were identified in the southern African birds which defined four haplotypes (A-D: GenBank accession numbers KM203404-7, Appendix 5.1) based on the control region sequences. One of these, haplotype A, was identical to a published sequence for birds collected from North Africa, Ethiopia and South Africa (haplotype 30, GenBank accession number AJ566879, Godoy *et al.* 2004). The three Ethiopian Bearded Vultures all had a single haplotype (A). Cytochrome b sequences (813 base pairs) generated for 11 specimens representative of the four control region haplotypes had an identical haplotype

(GenBank accession number KM203403), therefore no further analyses were conducted on the cytochrome b data.

AMOVA indicated no significant partitioning of genetic variation when the populations from sub-Saharan Africa were considered as a single group with 89% of the variation accounted for by the within-population component ($\Phi_{ST}=0.11$, $P=0.11$). When the Ethiopian samples were grouped separate from the southern African samples, the largest portion of variation remained within population (84%) with no significant variation between Ethiopia and southern Africa ($\Phi_{CT}=0.07$, $P=0.28$).

For the bootstrap analysis, sampling 37 individuals from southern Africa should have recovered an average of 7.86 different haplotypes if diversity in southern Africa was the same as on the Iberian Peninsula. Our finding of only four control region haplotypes (A-D) suggests a significant deficit in haplotype diversity in southern Africa ($P=0.0025$).

The haplotype network is presented in Figure 5.1. Our four haplotypes were closely related with three mutational steps separating the two most divergent haplotypes (D and B). The haplotypes retrieved in the current study group closely with haplotypes from birds sampled in North Africa, southern Africa and Ethiopia (AJ566879, haplotype 30, Godoy *et al.* 2004, our haplotype A) and Ethiopia (AJ566878, haplotype 29, Godoy *et al.* 2004). The haplotype network corresponded well with the maximum likelihood topology in Appendix 5.2.

Discussion

The evidence presented here suggests that apart from the known environmental threats to Bearded Vultures in southern Africa (Krüger *et al.* 2006, Chapter 6), genetic diversity is already considerably reduced. Uncertainties also exist regarding the number of subspecies or Evolutionarily Significant Units that should be recognized and the connectivity amongst regional populations, an important consideration in the management of the species.

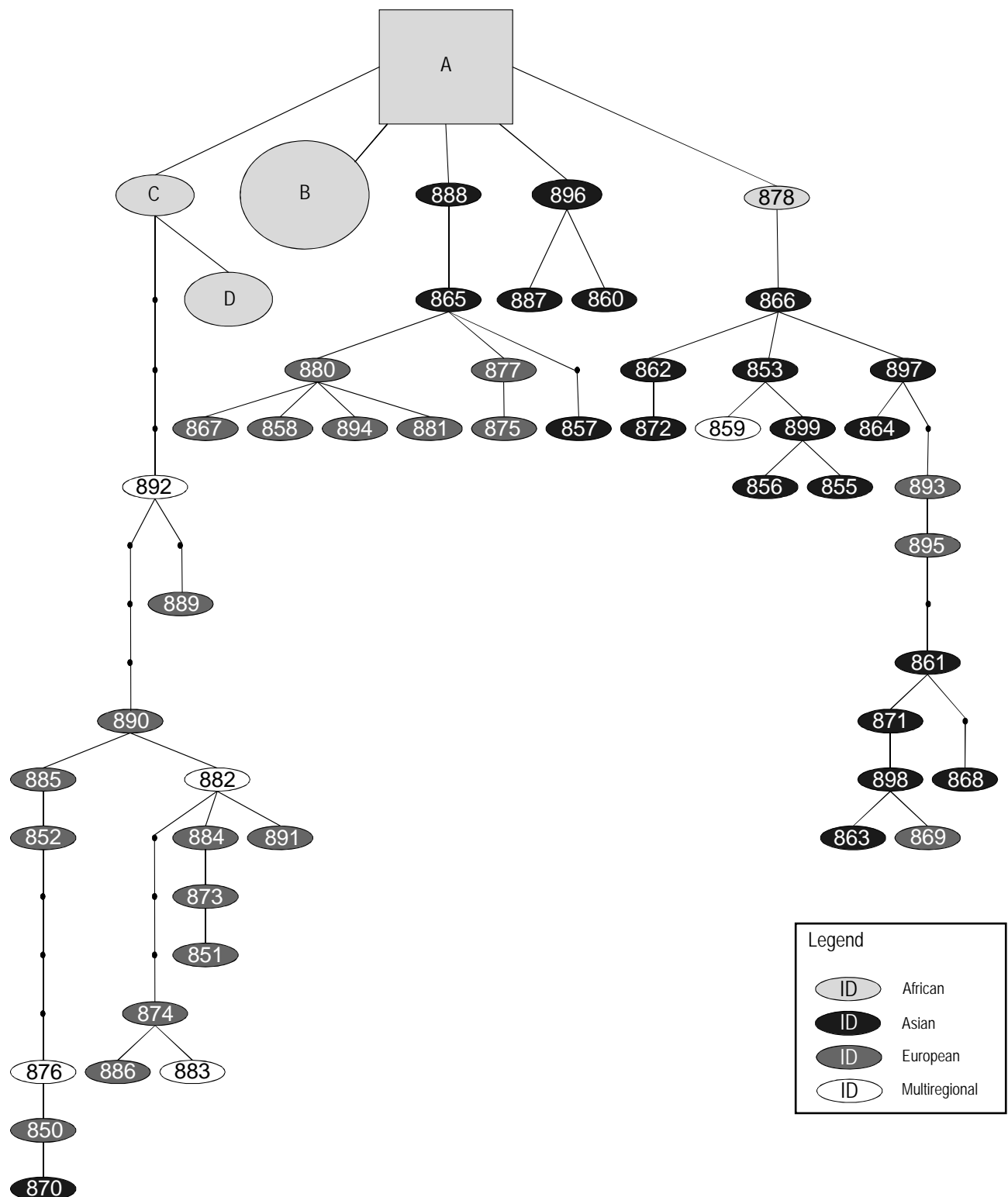


Figure 5.1 Haplotype network demonstrating the relationships between haplotypes generated by Godoy *et al.* (2004) and the present study. Haplotypes generated in the present study are indicated in grey shading. Haplotypes generated by Godoy *et al.* (2004) are shaded by sampling location and all have the prefix 'AJ566'. For details on haplotypes A to D refer to Appendix 5.1.

Our samples from Ethiopia and southern Africa group with samples from Africa, Europe, Asia and the Middle East. This clustering resolves the uncertainties of the Godoy *et al.* (2004) study, and strengthens their suggestion that Bearded Vultures should be managed as a single panmictic population due to the absence of significant differences in life history traits, morphology, habitat, behaviour or genetics across geographic regions. Although it may be difficult to conceive of high levels of connectivity between populations in Africa south of the Sahara Desert and Europe/Asia, these results, based on a mitochondrial marker, are unambiguous. The haplotype network suggests that the African haplotypes, particularly type A, are major links within the network and may well link the two clades identified by Godoy *et al.* (2004). This diversity pattern hints at Africa being the ancestral population, with the possibility that the movement of birds took place across the Horn of Africa (Somali Peninsula) rather than directly across the desert.

The southern African population is subject to a range of threats that are resulting in a continued decline (Krüger *et al.* 2006, Krüger *et al.* 2014, Chapters 2, 3 and 4). The low diversity at the mitochondrial level suggests these threats have had a real impact on the genetics of this critically endangered population. Similar levels of low genetic variability (haplotype diversity) have been found in other endangered raptors such as the Bonelli's Eagle *Hieraaetus fasciatus* (Cadahía *et al.* 2007), the Spanish Imperial Eagle *Aquila adalberti* (Martínez-Cruz *et al.* 2004), and the Black Harrier *Circus maurus* (Fuchs *et al.* 2014) and more specifically in other vultures; the Eurasian Black Vulture *Aegypius monachus* (Poulakakis *et al.* 2008), Egyptian Vulture *Neophron percnopterus* (Kretzmann *et al.* 2003) and Old World vultures (Lerner and Mindell 2005). These low levels of diversity have been ascribed to recent demographic declines mainly as a result of human pressure or population fragmentation. Other factors that may explain the low diversity in a population include small population size, drastic population size fluctuations over time, limited time since it diverged from its closest relative for genetic variation to appear, long term isolation from the East African population, repeated bottlenecks and a selective sweep (Roques and Negro 2005, Fuchs *et al.* 2014). The most likely explanation for the low diversity in the

southern African population is the drastic range reduction experienced by the population over the past three centuries attributed to anthropogenic factors resulting in a low effective population size (see Chapters 3 and 4). As such, significant concerns exist regarding the long-term viability and management of this isolated population.

Reduced diversity may decrease the population's fitness or limit the long term capacity of the population to respond to environmental challenges or chance environmental or demographic events in the short term and thus affecting survival and reproduction (Alexandre *et al.* 2007) in the long term. Therefore, for the long term persistence of the Bearded Vulture in southern Africa it is essential to maintain an adequate population size and high levels of genetic diversity.

Although translocations are not currently part of the management of this population, the possibility of augmenting the southern African population has been considered. From previous translocations in Europe, it is clear that this could be an effective management strategy (see Hirzel *et al.* 2004, Schaub *et al.* 2009). Given that the Ethiopian population appears to be large (Mundy *et al.* 1992) and shares an otherwise unique haplotype with southern Africa, individuals from Ethiopia may be used to supplement the southern African population in areas where the habitat is suitable.

Major changes to the management strategy of a species threatened with extinction should be carefully deliberated based on several lines of evidence. Although the mitochondrial DNA shows that birds from southern Africa and Ethiopia share haplotypes, it is imperative to add nuclear markers which will further inform questions such as whether connectivity between East and southern Africa is ongoing (gene flow), whether populations are inbred, as well as whether nuclear diversity is similarly low.

The information presented here is vital in guiding management decisions on the future of Bearded Vultures in southern Africa, and the consideration of exchange of individuals with other countries to ensure that sufficient genetic variability is maintained.

Further management options of increasing population size by maximizing the reproductive rate through improving the environment and protecting the population from environmental changes, disease and persecution must also be considered.

Acknowledgements

Rina Groenewald and the Central Analytical Facility at Stellenbosch University are thanked for assistance with the laboratory work. This work was financially and logistically supported by stipends from the DST-NRF Centre of Excellence for Invasion Biology and Ezemvelo KwaZulu-Natal Wildlife. Paulette Bloomer is thanked for providing primers. Arjun Amar, Rebecca Kimball, Rauri Bowie and an anonymous reviewer are thanked for their comments on the manuscript.

References

- Alexandre R, Couvet D and Sarrazin F (2007) Integration of demography and genetics in population restorations. *Ecoscience* 14: 463–471. doi:10.2980/1195-6860(2007)14 [463: IODAGI]2.0.CO;2.
- Ash J and Atkins J (2009) Birds of Ethiopia and Eritrea: An Atlas of Distribution. Christopher Helm, London.
- Birdlife International. (2014) IUCN Red List for birds. Downloaded from <http://www.birdlife.org> on 05/08/2014.
- Boshoff AF, Vernon CJ and Brooke RK (1983) Historical atlas of the diurnal raptors of the Cape Province (Aves: Falconiformes). *Ann Cape Prov Mus (Nat Hist Ser)* 14: 173-297.

- Cadahía L, Negro LL and Urios V (2007) Low mitochondrial DNA diversity in the endangered Bonelli's Eagle (*Hieraaetus fasciatus*) from SW Europe (Iberia) and NW Africa. *J Ornithol* 148: 99–104.
- Clement M, Posada D and Crandall KA (2000) TCS: a computer program to estimate gene genealogies. *Mol Ecol* 9: 1657-1659.
- Excoffier L, Laval G and Schneider S (2005) Arlequin ver. 3.0: An integrated software package for population genetics data analysis. *Evol Bioinform Online* 1: 47-50.
- Fuchs J, Simmons RE, Mindell DP, Bowie RCK and Oatley G (2014) Lack of mtDNA genetic diversity in the Black Harrier *Circus maurus*, a Southern African endemic. *Ibis* 156: 227–230.
- Godoy JA, Negro JJ, Hiraldo F and Donázar JA (2004) Phylogeography, genetic structure and diversity in the endangered bearded vulture (*Gypaetus barbatus*, L.) as revealed by mitochondrial DNA. *Mol Ecol* 13: 371-390.
- Hiraldo F, Delibes M and Calderón J (1984) Comments on the taxonomy of the bearded vulture *Gypaetus barbatus* (Linnaeus, 1758). *Bonn Zool Beitr* 35: 91-95.
- Hirzel AH, Posse B, Oggier P-A, Crettenand Y, Glenz C and Arlettaz R (2004) Ecological requirements of reintroduced species and the implications for release policy: the case of the bearded vulture. *J Appl Ecol* 41: 1103-1116.
- Irwin DM, Kocher TD and Wilson AC (1991) Evolution of the Cytochrome b Gene of Mammals. *J Mol Evol* 32: 128-144.
- Johnson JA, Gilbert M, Virani MZ, Asim M and Mindell DP (2008) Temporal genetic analysis of the critically endangered oriental white-backed vulture in Pakistan. *Biol Conserv* 141: 2403-2409.
- Joly S, Stevens MI and Jansen van Vuuren B (2007) Haplotype networks can be misleading in the presence of missing data. *Syst Biol* 56: 857-862.

- Kocher TD, Thomas WK, Meyer A, Edwards SV, Paabo S, Villablanca FX and Wilson AC (1989) Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proc Natl Acad Sci USA* 86: 6196-6200.
- Kretzmann MB, Capote N, Gautschi B, Godoy JA, Donázar JA and Negro JJ (2003) Genetically distinct island populations of the Egyptian vulture (*Neophron percnopterus*). *Conserv Gen* 4: 697–706.
- Krüger S (*in press*) Bearded Vulture. In: Taylor MR (editor) The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. BirdLife South Africa, Johannesburg.
- Krüger S, Piper S, Rushworth I, Botha A, Daly B, Allan D, Jenkins A, Burden D and Friedmann Y (editors) (2006) Bearded Vulture (*Gypaetus barbatus meridionalis*) Population and Habitat Viability Assessment Workshop Report. Conservation Breeding Specialist Group (SSC/IUCN)/CBSG Southern Africa, Endangered Wildlife Trust, Johannesburg.
- Krüger SC, Allan DG, Jenkins AR and Amar A (2014) Trends in territory occupancy, distribution and density of the Bearded Vulture *Gypaetus barbatus meridionalis* in southern Africa. *Bird Conserv Int* 24: 162-177. doi:10.1017/S0959270913000440.
- Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R, Thompson JD, Gibson TJ and Higgins DG (2007) Clustal W and Clustal X version 2.0. *Bioinformatics* 23: 2947-2948.
- Lerner HRL and Mindell DP (2005) Phylogeny of eagles, Old World vultures, and other Accipitridae based on nuclear and mitochondrial DNA. *Mol Phylog Evol* 37: 327–346.
- Lowe AJ, Boshier D, Ward M, Bacles CFE and Navarro C (2005) Genetic resource impacts of habitat loss and degradation; reconciling empirical evidence and predicted theory for neotropical trees. *Heredity* 95: 255-273.

- Margalida A, Heredia R, Razin M and Hernandez M (2008) Sources of variation in mortality of the Bearded Vulture *Gypaetus barbatus* in Europe. *Bird Conserv Int* 18: 1-10.
- Martínez-Cruz B, Godoy JA and Negro JJ (2004) Population genetics after fragmentation: the case of the endangered Spanish imperial eagle (*Aquila adalberti*). *Mol Ecol* 13: 2243–2255.
- Mundy P, Butchart D, Ledger J and Piper S (1992) The Vultures of Africa. Russel Friedman Books cc, Johannesburg.
- Poulakakis N, Antoniou A, Mantziou G, Parmakelis A, Skartsi T, Vasilakis D, Elorriaga J, de la Puente J, Gavashelishvili A, Ghasabyan M, Katzner T, McGrady M, Batbayar N, Fuller M and Natsagdorj T (2008) Population structure, diversity, and phylogeography in the near-threatened Eurasian black vultures *Aegypius monachus* (Falconiformes; Accipitridae) in Europe: insights from microsatellite and mitochondrial DNA variation. *Biol J Linn Soc* 95: 859–872.
- Roques S and Negro JJ (2005) MtDNA genetic diversity and population history of a dwindling raptorial bird, the red kite (*Milvus milvus*). *Biol Conserv* 126: 41–50.
- Schaub M, Zink R, Beissmann H, Sarrazin F and Arlettaz R (2009) When to end releases in reintroduction programmes: demographic rates and population viability analysis of bearded vultures in the Alps. *J Appl Ecol* 46: 92-100.
- Tamura K, Stecher G, Peterson D, Filipski A and Kumar S (2013) MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. *Mol Biol Evol* 30: 2725-2729.

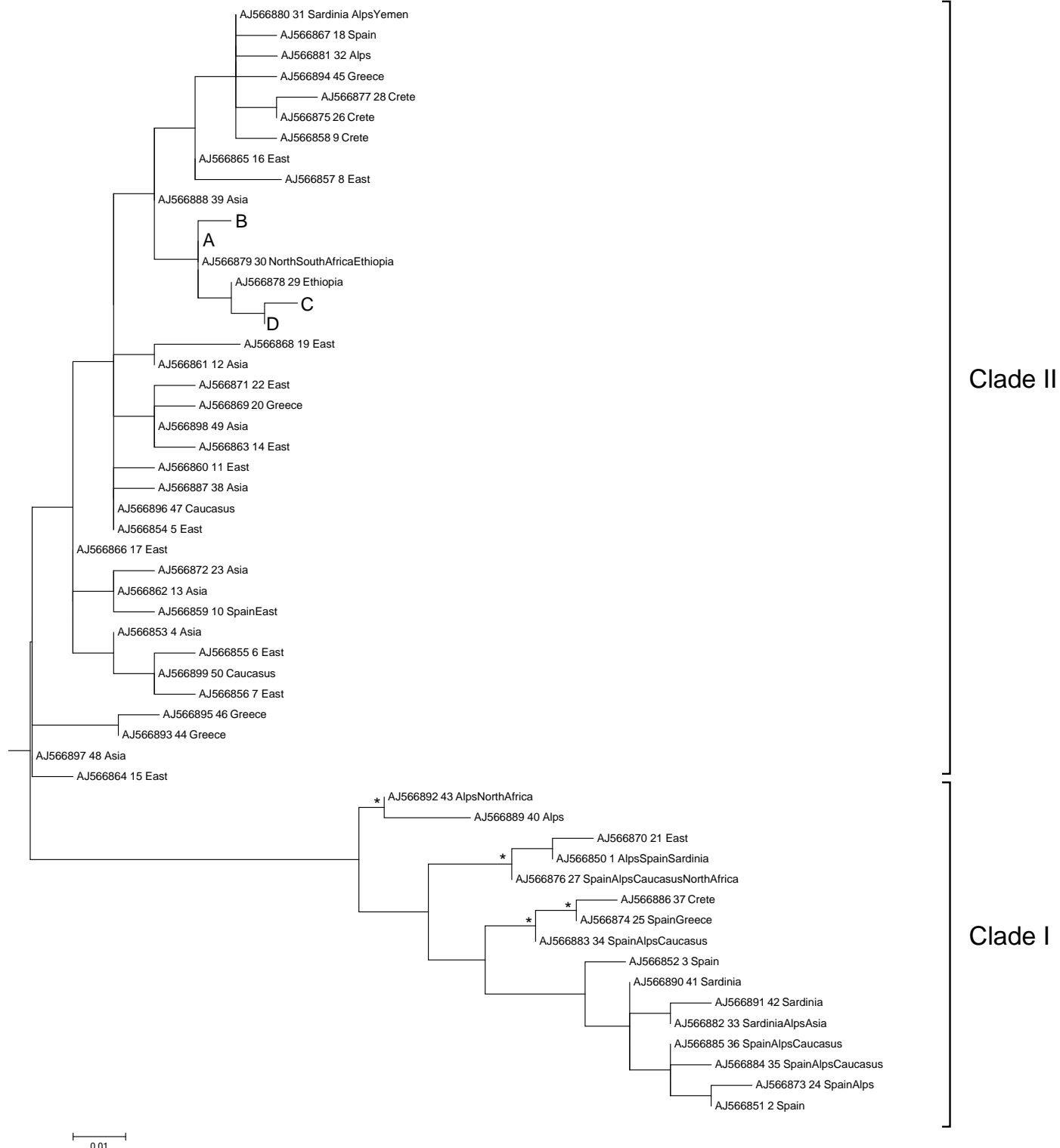
Appendices

Appendix 5.1 Summary list of samples used in this study. The southern African samples were collected by S.C. Krüger in the KwaZulu-Natal (KZN), Free State and Eastern Cape provinces of South Africa and the Maseru, Thaba-Tseka and Mokhotlong Districts of Lesotho. Ethiopian samples were provided by the Peregrine Fund.

Sample ID	Locality	Country	Year	Tissue	Haplotype*
BV001	Southern Drakensberg, KZN	South Africa	2006	blood	B
BV002 [†]	Southern Drakensberg, KZN	South Africa	2007	blood	B
BV003	Southern Drakensberg, KZN	South Africa	2007	blood	A
BV004 [†]	Southern Drakensberg, KZN	South Africa	2009	blood	D
BV005 [†]	Southern Drakensberg, KZN	South Africa	2010	blood	B
BV006 [†]	Southern Drakensberg, KZN	South Africa	2009	blood	B
BV007 [†]	Maseru District	Lesotho	2012	blood	B
BV008	Southern Drakensberg, KZN	South Africa	2009	blood	D
BV009 [†]	Northern Drakensberg, KZN	South Africa	2011	blood	C
BV010	Northern Drakensberg, KZN	South Africa	2010	blood	A
BV011	Free State Province	South Africa	2004	feather	C
BV012	Central Drakensberg, KZN	South Africa	2002	muscle	B
BV013 [†]	Thaba-Tseka District	Lesotho	2008	muscle	D
BV014	Central Drakensberg, KZN	South Africa	2009	muscle	D
BV015 [†]	Southern Drakensberg, KZN	South Africa	2011	blood	B
BV016 [†]	Southern Drakensberg, KZN	South Africa	2009	blood	A
BV017	Mokhotlong District	Lesotho	2008	blood	B
BV018	Southern Drakensberg, KZN	South Africa	2009	blood	A
BV019	Southern Drakensberg, KZN	South Africa	2003	feather	B
BV020	Mokhotlong District	Lesotho	2007	feather	B
BV021	Northern Drakensberg, KZN	South Africa	2011	feather	A
BV022	Central Drakensberg, KZN	South Africa	2008	feather	B
BV023	Northern Drakensberg, KZN	South Africa	2009	feather	D
BV024	Southern Drakensberg, KZN	South Africa	2010	feather	B
BV025	Southern Drakensberg, KZN	South Africa	2000	feather	B
BV026	Southern Drakensberg, KZN	South Africa	2007	feather	B
BV027	Southern Drakensberg, KZN	South Africa	2010	feather	A
BV028	Southern Drakensberg, KZN	South Africa	2010	feather	A
BV029	Northern Drakensberg, KZN	South Africa	2010	feather	C
BV030	Southern Drakensberg, KZN	South Africa	2009	feather	B
BV031	Ethiopia	Ethiopia	2001	blood	A
BV032	Ethiopia	Ethiopia	2001	blood	A
BV033	Ethiopia	Ethiopia	2001	blood	A
BV034	Central Drakensberg, KZN	South Africa	2012	feather	A
BV035	Eastern Cape Province	South Africa	2012	muscle	B
BV036	Northern Drakensberg, KZN	South Africa	2012	blood	A
BV037 [†]	Central Drakensberg, KZN	South Africa	2012	blood	D
BV038	Northern Drakensberg, KZN	South Africa	2012	blood	A
BV039	Central Drakensberg, KZN	South Africa	2012	blood	A
BV040 [†]	Central Drakensberg, KZN	South Africa	2012	blood	C

*Haplotype A was identical to Haplotype 30, GenBank accession number AJ566879, Godoy *et al.* (2004).

[†]Sub-sample of individuals for which Cytochrome b sequences (813 base pairs) were generated.



Appendix 5.2 Maximum likelihood topology generated under the evolutionary model that best fitted the data. Haplotypes A to D represent those detected in the present study while GenBank accession numbers are given for haplotypes generated by Godoy *et al.* (2004). Nodes that are supported by more than 70% bootstrap support (derived from 10,000 replicates) are indicated by *.

**Chapter 6: Poisoning increases the extinction risk of the
Bearded Vulture *Gypaetus barbatus* in southern
Africa**



Photo 6 A selection of Bearded Vultures found dead from poisoning (left) and power line collisions (right)

Chapter 5 will be submitted to Oryx.

Krüger SC and Amar A. Poisoning increases the extinction risk of the Bearded Vulture *Gypaetus barbatus* in southern Africa.

Abstract

This study aims to identify the demographic and environmental constraints on Bearded Vulture in southern Africa, a population which has declined dramatically over the past few decades. We use surveys undertaken during 2000-2014 to obtain the necessary demographic data to model population trends using VORTEX population viability analysis software. Nesting success for pairs attempting to breed was relatively high (76%), but pairs did not attempt to breed every year thus lowering the productivity of the population to 55%, which appeared to contrast with previous surveys, suggesting the productivity may have declined over the last three decades. Survival rates estimated from marked birds were low for adults in particular (86%), in relation to other raptor species with similar life histories. Human activities (69%) and power line collisions ($n=21\%$) were the primary mortality factors of birds found dead ($n=19$), with poisoning alone accounting for 90% of marked birds found dead ($n=10$). Using our population model with existing demographic rates to hind cast population size between 1960–2000 resulted in a much lower population growth rate ($\lambda=0.91$) than observed, predicting far fewer individuals in the population (*ca.* 1) than currently observed (*ca.* 368-408). This suggests a more gradual or more recent declines in demographic parameters. Projecting forward, based on current demographic rates, our stochastic models predicted a negative growth rate over the next 50 years ($\lambda=0.99$) with an 89% chance of extinction. Modelling various management scenarios such as increasing productivity, decreasing mortality and supplementation, only resulted in a positive population growth rate ($\lambda=1.06$) with a probability of extinction of <0.50 (the minimum requirements), if mortality was reduced by 40%, productivity was increased by 15% and the population was supplemented by four individuals. We conclude that unnatural mortalities, poisoning in particular, are the cause of poor population growth of the Bearded Vulture in southern Africa and recommend actions to address the threat of poisoning in particular as the priority intervention. Such actions would also help other vulture species in the region which are also likely to be suffering from the same threat.

Introduction

Populations that are small and geographically isolated have a heightened extinction risk (Gaston 1994). Population size has been shown to be the major determinant of persistence in populations of a variety of animal species (Brown 1971, Jones and Diamond 1976, Diamond *et al.* 1987, Pimm *et al.* 1993, Soulé *et al.* 1988, Rosenzweig 1995, Fouloupoulos and Ives, 1999). Small populations are more vulnerable to demographic stochasticity, local catastrophes, slow rates of adaptation and inbreeding (Brown 1995, Lande 1999). In addition species with low reproductive rates are less able to compensate for increased mortality with increased fecundity, making them more vulnerable to population extinction (MacArthur and Wilson 1967, Saether and Bakke 2000).

Populations of large raptors in particular are sensitive to reductions in demographic rates, notably survival rates (Smart *et al.* 2010), particularly when their populations are small. Vultures are among the most endangered raptors, partly due to their extremely low reproductive rates (Newton 1998, Ogada *et al.* 2012). The Bearded Vulture population in southern Africa is a geographically isolated population restricted to the Maloti-Drakensberg mountains. The population has declined in distribution, density and territorial occupancy in the past few decades (Krüger *et al.* 2014a, Chapter 2). As a result the species has been uplisted to Critically Endangered in South Africa and Lesotho (Krüger *in press*) indicating that it faces an extremely high risk of extinction in the wild as a result of a reduction in population size and geographic range and the continuing threats to the species (IUCN 2001). In this chapter, we examine the demographic parameters of this population including age structure, nesting success and survival rates and use these parameters to quantify the extinction risk of the population, identify the mechanisms responsible and set conservation priorities to address the decline.

Population viability analysis (PVA) provides a quantitative means for predicting the probability of extinction and prioritizing conservation needs by determining which demographic parameters are most influential in population persistence (Shaffer 1981, Gilpin

and Soulé 1986, Beissinger and McCullough 2002). A simple PVA was undertaken for the southern African Bearded Vulture in 2006 (Krüger *et al.* 2006). However the lack of reliable and current data made it difficult to produce accurate population projections. This study aims to address these previous gaps in knowledge enabling us to improve on the original modelling exercise and calculate a more realistic population growth rate and explore which conservation interventions might successfully reverse this declining trend.

Population growth rates are primarily influenced by natality and mortality. In long lived raptor species population growth is usually most sensitive to mortality rates. Therefore in this study we explore the primary causes of mortality. An investigation into the decline of the Bearded Vulture in the 1980s determined that poisoning was the primary mortality factor as well as gin traps and direct persecution (Brown 1991). More recent reports suggest that poisoning still affects vultures (Boshoff *et al.* 1998). This poisoning is linked to traditional medicine (Ngwenya 2001, Mander *et al.* 2007), scavenger control (Brown 1991) and the assumed threat of vultures to livestock in Lesotho (S. Zwakala *pers. comm.*). Collisions with power lines were found to be a minor cause of mortality in the past, accounting for less than 10% of deaths in southern Africa (Brown 1991) and 18% of deaths in Europe (Margalida *et al.* 2008). Mortality rates from power line collisions are likely to be higher than recorded because of the expanding transmission and distribution networks (Kalipeni 1994, Energy Sector Policy of the AfDB group 2012) and the fact that collision carcasses are often not found because of the inaccessible terrain and the carcasses landing some distance away from the lines or being scavenged. We investigate the current mortality factors by assessing the fate of GPS tracked individuals. Although the proportion of tracked individuals in the population is low, the sample size does provide an indication of the causes and rates of mortality. These data combined with age distribution data from feeding sites, also provide an indication of age specific survivorship rates.

In this chapter we also explore nesting success which is an important component of natality. Krüger *et al.* (2014a, Chapter 2) suggested that anthropogenic influences were

driving the abandonment of Bearded Vulture territories, particularly on the periphery of the breeding range. In Chapter 3 we investigated the mechanisms of territorial abandonment and found strong support for anthropogenic factors, particularly the density of power lines and settlements driving the decline. Neither study, however, investigated the productivity of the population although both recognized that lower recruitment could in theory be the mechanism of these findings, with the population shrinking back to their core range with sub-optimal territories being abandoned. Understanding levels of productivity, particularly in relation to historic rates, could usefully illuminate how relevant this demographic parameter is to the overall population decline. Historical breeding records of the southern African Bearded Vulture population indicate that several monitored pairs bred annually (Penzhorn 1969). Subsequent records indicate that all monitored pairs attempted to breed annually with a relatively high nesting success rate (0.89 young/pair/year) (Brown 1997). In other parts of their global range, however, the species does not breed every year and has an average nesting success rate of 0.60 young/pair/year (Brown 1977, Brown *et al.* 1982, Heredia 1991, Terasse 1991, Margalida *et al.* 2003).

In this study we aim to establish several key demographic parameter estimates and then combine these in a PVA. We aim to improve our current estimates for 1) age structure 2) age specific survival rates, 3) nesting success (and whether this has changed from historical records), and 4) causes of mortality. We estimate the likely future population growth rate with these current demographic rates, and lastly we identify the most plausible conservation interventions required to achieve the minimum conservation objectives stated in the Biodiversity Management Plan for the species (Krüger 2013), specifically to stabilise the population in the short term.

Methods

We monitored the Bearded Vulture population in southern Africa from 2000-2014 throughout its range with the emphasis on detecting territorial pairs through aerial and foot surveys of

breeding sites (Kruger *et al.* 2014a), determining the age class structure of the population through foot and vehicle surveys, and recording mortalities of marked birds. In order to obtain a more representative sample of territory status and age structure, surveys were conducted in both the core and periphery of the species' range. The core range (Figure 6.1) focussed on the breeding portion of the population and was defined as the area containing territories occupied by Bearded Vulture ($n=109$ from Krüger *et al.* 2014a, Chapter 2) that were surrounded by at least five quarter degree squares that contained occupied Bearded Vulture territories.

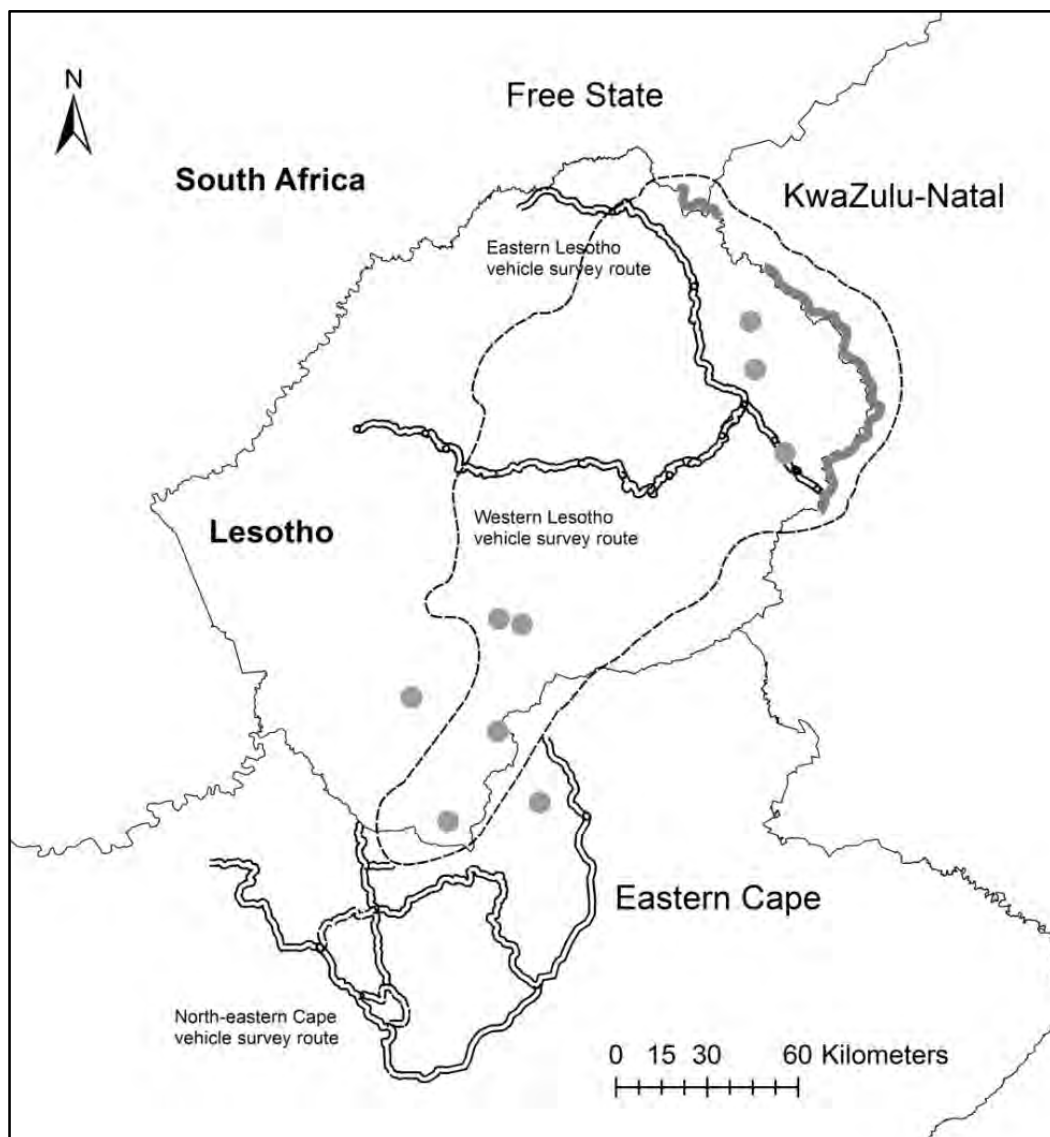


Figure 6.1 The location of road survey routes (==) and foot survey routes (•) in relation to the core breeding range (--) within the Maloti Drakensberg mountains of Lesotho and South Arica.

Age Structure

The percentage of non-adults in the population was required to more accurately estimate the current population size and was calculated from foot surveys undertaken in the core breeding range and vehicle surveys performed throughout the range (Figure 6.1). Each Bearded Vulture recorded during the two survey methods was classed as either a non-adult (post-fledging to <6 years) or an adult (≥ 6 years), based on plumage characteristics; with non-adults primarily dark in colour and adults easily identified by their orange coloured chest and white head (Figure 4.2). Since the habitat and topography were similar in all regions, it was assumed that 'visibility' of the birds was similar throughout.

Foot surveys (n=169 observation hours) were conducted in 2012 following the method of Brown (1992) and Krüger *et al.* (2014a, Chapter 2) with the number of individuals and their ages recorded along with the duration of the survey. Vehicle surveys were also conducted in 2012 following the method of Brown (1992) with the number of individuals and their ages recorded along with the distance and the duration of each vehicle survey. The average speed of travel during vehicle surveys was 20 km/h. A total of 2,231 km of vehicle surveys were driven; 816 km in July in the Lesotho highlands west of the Senqu River, 799 km in September in Lesotho east of the Senqu River, and 616 km in December in the northern part of the Eastern Cape (Figure 6.1). These surveys were conducted by S. Krüger who was accompanied by the original historical surveyor (C. Brown) for the first survey which further ensured consistencies between the two survey periods.

Although surveys were also conducted at supplementary feeding sites (n=108 observation days), we chose to exclude these data from our calculations because Margalida *et al.* (2011) found that surveys at supplementary feeding sites did not reflect the age structure of the Bearded Vulture population and significantly over-estimated the proportion of juveniles and under-estimated the numbers of sub-adults and adults.

Although the survey methods to obtain age structure were similar to those of Brown (1997), we were not able to infer the proportion of young birds in the population based on

inter-nest distances as per his method because our data showed that the proportion of non-adults in an area was not inversely related to the density of adult birds. We therefore calculated the age structure using a weighted average percentage of non-adults sighted during foot and vehicle counts. We expected our foot count data to bias the results by only being conducted in the core range where the proportion of adults is likely to be over-estimated. Since the core range constituted over half (56%) of the total range and since the survey effort/total number of birds sighted in the core range was twice that of the vehicle counts, we used a weighting of 1(foot counts): 4 (vehicle counts) when calculating the average percentage of non-adults.

Productivity

We calculated the productivity of the population using data collected on breeding activity between 2000-2014 at the 109 territories occupied by Bearded Vulture in southern Africa. The criteria used to classify the breeding activity described below are summarized in Table 6.1. In any one year, we defined an occupied territory as one where at least one adult was flushed off the cliff or seen flying or roosting in the area, entering a pothole or overhang on the cliff; if a chick or fledgling was seen; or if there was fresh whitewash and plant material (sticks) on the nest indicating recent use attributed to this species based on the location of the whitewash and the type of nest structure (see also Krüger *et al.* 2014a, Chapter 2). Territories where no activity had been recorded for at least four consecutive years were considered abandoned (see also Krüger *et al.* 2014a, Chapter 2) and were not included in the calculation of laying rate and nesting success (as described below).

We measured productivity at the population level as the mean number of fledglings raised per territorial pair (occupied territory), including breeding failures and taking into account that no more than one nestling could be reared per breeding attempt (Ferrer *et al.* 2014). For this long-lived raptor that maintains the same territory throughout the year and does not necessarily breed every year (see Chapter 4), there can be a large difference

between nesting success per territorial pair and nesting success per laying pair. For this reason, our productivity calculations took into account; i) *laying rate*- defined as the number of years with egg laying per number of monitored years per occupied territory (as defined by Ferrer *et al.* 2014), and ii) *nesting success*- defined as the proportion of laying pairs that raise young to the age of fledging (Steenhof and Newton 2007).

Table 6.1 Classification criteria for determining Bearded Vulture productivity in southern Africa. Criteria are based on the definitions provided by Steenhof and Newton (2007) and methods used by Krüger *et al.* (2014a, Chapter 2) and Ferrar *et al.* (2014) to determine the fecundity of Bearded Vulture in the Spanish Pyrenees.

Classification	Criteria
Occupied territory	Presence of at least one adult flying or roosting in the area or entering a pothole; or a chick/fledgling; or fresh whitewash and plant material (sticks) on the nest
Abandoned territory	A territory where no activity was recorded for at least four consecutive years
Territorial pair	Two adult birds present in an occupied territory
Laying pair	Two adults in an occupied territory that appeared to be paired or one or more adults engaged in territorial defence, nest affinity, or other reproductive-related activity
Laying rate	Number of years with egg laying per number of monitored years
Nesting success	Proportion of laying pairs that raise young to the age of fledging
Productivity	Mean number of fledglings raised per territorial pair, including breeding failures and taking into account that no more than one nestling could be reared per breeding attempt (= % laying rate x % nesting success/100)

Data on productivity was obtained from both ground and aerial helicopter surveys. Ground surveys were undertaken primarily on foot, and by road, using 20-60 X telescopes at between 200–1,000 m. Breeding territories were observed between first and last light for an average of four hours or until the type of breeding activity was confirmed. Aerial helicopter surveys were undertaken at approximately 100-500 m from the cliff edge at an average

flying speed of 70-80 km/h with a minimum of two observers looking out of the port side of the aircraft.

Year-to-year fluctuations in nesting success and productivity are common in raptors (Steenhof and Newton 2007) therefore in order to reduce 'measurement error' (the misclassification of the status of a particular pair or breeding territory as a result of field situation, weather or observer inexperience) we used only occupied territories that had been surveyed at least seven times during the 14 survey years (*i.e.* $\geq 50\%$, $n=41$). Territories were surveyed in both the core and periphery of the breeding range to reduce sampling error which may occur when the pairs observed are not representative of the entire population.

Laying activity was confirmed if an occupied territory contained two birds that appeared to be paired or one or more adults engaged in territorial defence, nest affinity, or other reproductive-related activity. To calculate *nesting success* we used only data from occupied territories known to have laying pairs that were visited more than once during the breeding season ($n=35$) to avoid the danger of distorting the conclusions by using incomplete records. Nest checks had to be during the pre-laying or incubation stage and at the late-nestling or fledging stage to examine final nesting success measures.

Estimation of Survival Rates

We estimated age specific survival rates using data from birds marked with tracking devices. In total, twenty four birds were fitted with satellite Platform Transmitter Terminals (PTTs) between September 2007 and September 2012 in the Maloti-Drakensberg region of Lesotho and South Africa (see also Chapter 4). Four nestlings were fitted with 45 g solar-powered GPS-PTTs (North Star Science and Technology, LLC, Virginia, USA) prior to fledging and 20 individuals were caught at supplementary feeding sites and fitted with 70 g solar-powered GPS-PTT-100s (Microwave Telemetry Inc., Maryland, USA).

We chose months as our sampling unit to calculate survival rates because of the small sample size of marked individuals. We classified whether an individual was alive in a given month from date of marking based on GPS fixes received during that month up to and including July 2014. Only months that had data for the entire month were used. Our survival models included seven age classes. We calculated annual percentage survival per age class using: $(\phi_{a7} = d/m) * 12 * 100$; where ϕ is survival rate, $a7$ is age in seven age classes (0->6 years), d is the number of mortalities per age class and m is the number of months an individual was alive summed per age class which was multiplied by 12 to obtain an annual survival estimate and multiplied by 100 to convert this from a proportion into a percentage. We used 200 bootstrap replicates to generate standard deviations for age specific survival rates because of the small sample size of marked birds.

Quantifying Causes of Mortality

We collated all available information on the causes of mortality of Bearded Vultures found dead during the study period (2000-2014) including mortalities of both marked and unmarked birds. Using causes of mortality from marked birds alone is the best way to obtain unbiased data, although as a result sample size is usually compromised (González *et al.* 2007). We therefore included additional mortality records from databases of Ezemvelo KwaZulu-Natal Wildlife and the Wildlife Conflict Mitigation and Wildlife and Energy Programmes of the Endangered Wildlife Trust as well as information from questionnaire surveys undertaken in South Africa (Hiltunen 2008, Mander *et al.* 2007) and Lesotho (S. Piper, M. Shobana and S. Zwakala *pers. comm.*). Although estimating mortality causes from numbers of dead animals can be biased (Schaub and Pradel 2004), these data together with data from marked birds will provide the best possible indication of causes of mortality.

Where possible cause of death was established or confirmed by an autopsy which included X-Rays and toxicology, pathology, histology and mineral analysis tests. Individuals found dead were tested for pesticides/poisons as well as lead (Pb) levels in the bone. Bone

lead levels represent repeated and chronic exposure to lead, as bones are long-term repositories of lead (Pain *et al.* 1993, Gangoso *et al.* 2009). Vultures with lead levels of 10-20 µg/g have had abnormal or excessive exposure and absorption of lead, and those with levels of >20 µg/g have had chronic exposure (Gangoso *et al.* 2009), such as those that have died of lead poisoning (Pain *et al.* 2007).

Population Modelling

We modelled the population growth rates and the resulting population size of the southern African Bearded Vulture using VORTEX population viability analysis software (Lacy *et al.* 2005).

In a similar approach to Smart *et al.* (2010) and Evans *et al.* (2009), we used our model to firstly test whether we could re-capitulate the observed history of the population trajectory from 1960 to 2000 based on population estimates from Krüger *et al.* (2014a, Chapter 2) for the time periods 1960-1999 and 2000-2012, by using the current demographic estimates (productivity and age specific mortality) obtained in this study. Secondly we used current data on the status and demography of the population to compare hypothetical population trajectories over 50 years from 2000 to explore the likely future population trends and to test the effects of interventions aimed at increasing the population growth rate. These scenarios constituted; i) current population size and current demographic rates, ii) revised survival estimates for each age class removing the additive effect of unnatural mortalities, iii) increased productivity estimates, and iv) supplementation to explore the impact of captive breeding with subsequent introductions. For each scenario, we performed 1000 replicates during the simulated 50-year period. The parameter values used in the baseline models are detailed in Appendix 6.1.

Statistical Analyses

We tested whether there was a relationship between the location of the territory *i.e.* in the core or periphery of the range and the laying rate using a General Linear Model in R v.3.0.2. (R Core Team 2013) with an Arcsine square-root transformation of the percentage laying rate. We also tested whether there was a relationship between the location of the territory and nesting success. For this we used a Generalized Linear Model (binomial error structure and a logit link function) with the probability of success (1/0) as the response variable and location as the explanatory variable. The nest site was included as a random term as we had repeated measures for the same nest site over a number of years.

Results

Age Structure

A total of 169 hours were spent on foot surveys which was twice the number of hours spent on vehicle surveys (84 hours) (see Appendix 6.2 for vehicle survey details). On average, non-adults were encountered 14% of the time in the core breeding areas during foot surveys, whereas they were sighted on average 47% of the time during vehicle surveys, with a low percentage of sightings in the core range and a high percentage in the peripheral areas (Figure 6.2, Table 6.2). Based on the two survey methods, and weighting the foot survey data by survey effort and survey area respectively (*i.e.* essentially four orders of magnitude less than the vehicle surveys), we estimate that the population as a whole consists of, on average, 59.6% adults and 40.4% non-adults. This age structure was used to update the population estimate of 352-390 (Krüger *et al.* 2014a, Chapter 2) to 368-408 individuals.

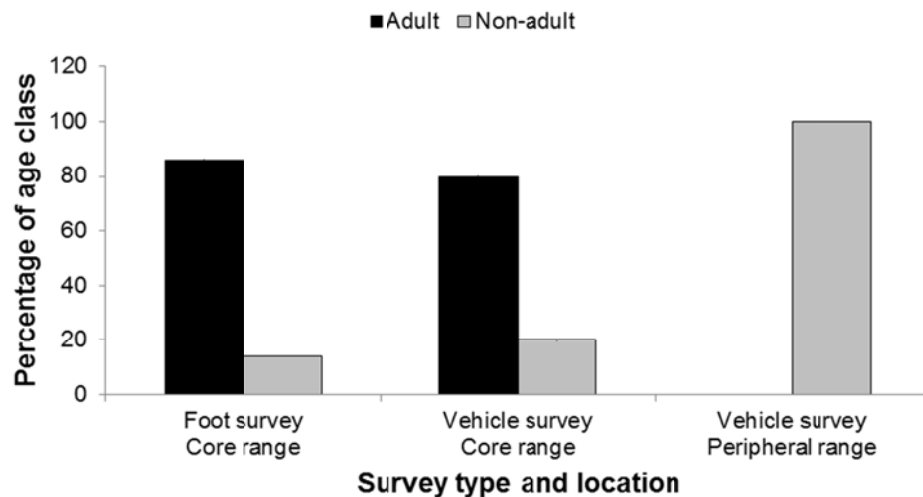


Figure 6.2 The percentage of adults and non-adults observed during foot and vehicle surveys in the core and periphery of the range of the Bearded Vulture in southern Africa.

Table 6.2 Age structure summary of the Bearded Vulture in southern Africa calculated from foot and road surveys (number of individuals sighted per 10 hours) conducted in the core and periphery of the range. Percentages are displayed in parentheses and are based on the total number of positive age classifications.

Survey type and location	Adult	Non-adult	Unknown
Foot survey (core)	2.55 (86%)	0.42 (14%)	0.71
Road survey (Western Lesotho, core range)	1.89 (100%)	0 (0%)	0
Road survey (Eastern Lesotho, core range)	3.35 (60%)	2.23 (40%)	0.37
Road survey (Eastern Cape peripheral range)	0 (0%)	0.39 (100%)	1.18
Road survey average	53%	47%	-

Productivity

Laying Rate

During 2000-2013, 437 visits were undertaken to 41 individual territories involving 389 visits to 35 sites in the core range and 48 visits to six sites in the peripheral range. The laying rate was 52% overall, 49% in core and 68% in the peripheral areas. These data suggest that the birds only breed every second year and pairs at peripheral sites attempt to breed more often

than in the core areas although this difference was marginally non-significant ($F_{1,39}=3.20$, $P=0.08$).

To further refine our data and ensure that the low rate of laying was not simply a function of observer inexperience, we sub-sampled eight sites that were surveyed by S. Krüger annually between 2008-2013. From these eight sites, three were in the core area in Lesotho and South Africa respectively and one was in the peripheral part of the range in each country. Results indicated that birds in occupied territories only attempted to lay 72% ($n=33$) of the time.

Nesting Success

A total of 76 laying pairs were monitored to determine nesting success. 35 different pairs were monitored in total; nineteen pairs were monitored for one year only, seven pairs for two years, three pairs for three years, four pairs for four years and one pair for seven and 11 years respectively.

The overall nesting success recorded in this study was 76% (Table 6.3). Two breeding failures were attributed to mate loss and the effects of fire respectively. Sites visited in the core of the range (62 nest visits to 30 different sites) had a higher nesting success (79%) than sites visited in the periphery (64%) of the range (14 nest visits to 4 different sites), although the relationship between nest location and nesting success was not significant ($\chi^2 = 0.81$, $df=1$, $P=0.37$).

Combining the laying rate (72%) from the sub-sample of eight sites monitored by S. Krüger together with the nesting success of laying pairs (76%), the productivity of the population was estimated at 0.55 young/pair/year (0.59 in the core and 0.40 in the periphery of the range). By comparison, combining the laying rate of the original sample of 41 sites (52%) with the nesting success of laying pairs (76%) resulted in a much lower productivity of 0.40 young/pair/year.

Table 6.3 A comparison between breeding success and productivity (taking into account laying rate) of the Bearded Vulture in southern Africa.

Location	Number of nests	Breeding success	Productivity
Entire range	34	76 % (n=76)	55 %
Core range	30	79 % (n=62)	68 %
Peripheral range	4	64 % (n=14)	46 %

Annual Survival Estimates and Causes of Mortality

Of the 24 Bearded Vultures fitted with satellite tags between 2007 and 2012, two experienced transmitter failures, two birds dropped their transmitters after 10 and 24 months respectively, and 10 individuals (50%, n=20) were found dead during the study period. The cause of death was established as a power line collision (n=1), and poisoning from pesticides (n=6) or lead (n=4) (Table 6.4, Figure 6.3). A further nine birds were reported dead during the study period as a result of poison (n=1), being trapped/caught (n=3), colliding with power lines (n=3) and natural causes (n=2) (Table 6.4, Figure 6.3). Three individuals recorded as poisoned were not confirmed through an autopsy because the carcasses were too autolysed but they were assumed to be poisoned based on the state of these birds in the field (lying face down with wings outstretched) being the same as all other birds confirmed poisoned. Human activities, either direct persecution through trapping/poisoning birds or indirect through poisoning (feeding on carcasses shot with lead or poisoned with carbamate insecticides meant for predator control) accounted for 69% of the deaths with poisoning alone accounting for more than half the mortalities recorded during the study period. The location of mortality events shows that these were widespread across the range of the population, with poisoning events occurring in Lesotho and all three provinces of South Africa (Figure 6.3).

Of the five poisoned birds that were tested for lead levels in the bone, 80% (n=4) had high levels of lead, of which two individuals showed a lead concentration to be indicative of

abnormal or excessive exposure and absorption of lead (10-20 $\mu\text{g/g}$) and two showed concentrations indicative of chronic exposure ($>20 \mu\text{g/g}$).

Table 6.4. The number of Bearded Vulture found dead during 2000-2014 where cause of death was either through i) being deliberately or accidentally poisoned, ii) colliding with power lines, iii) deliberately or accidentally trapped, or iv) natural causes.

Age Class	Cause of death				Total
	Poisoned	Power line	Trapped	Natural	
Fledgling (0-1 year)	1*	0	1	0	2 (11%)
Juvenile (1-2 years)	1	2	2	1	6 (32%)
Immature (2-3 years)	2* (1 lead)	1	0	0	3 (16%)
Immature (3-4 years)	2 (1 lead)	0	0	0	2 (11%)
Sub-adult (4-5 years)	1 (1 lead)	0	0	0	1 (5%)
Sub-adult (5-6 years)	0	0	0	1	1 (5%)
Adult (>6 years)	3* (1 lead)	1	0	0	4 (21%)
Total	10 (53%)	4 (21%)	3 (16%)	2(11%)	19

*Poisoning assumed (see text for details)

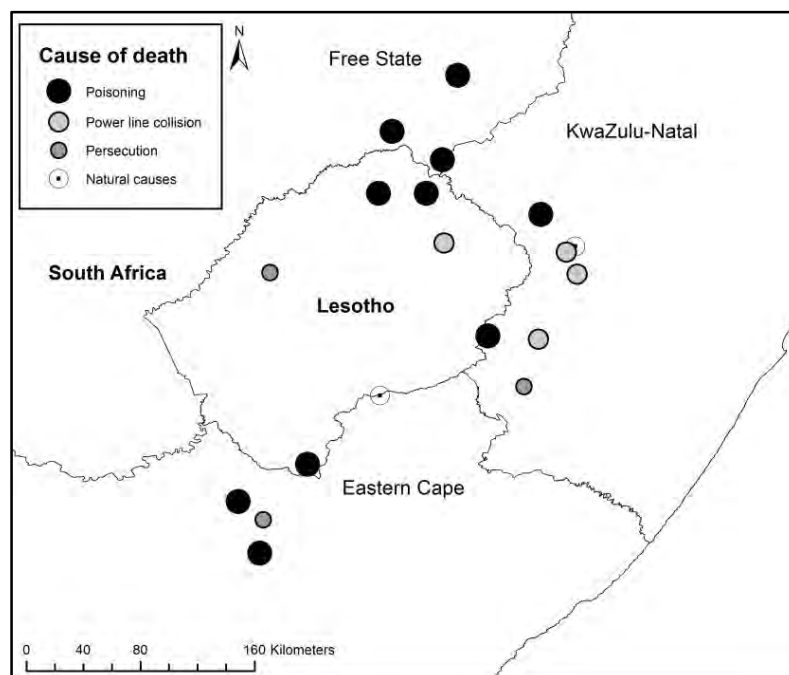


Figure 6.3 The location of mortality events depicted by cause of death showing the distribution of mortalities across the population's range.

Age specific survival estimates were based on 49.83 years data from the 22 marked individuals of seven age classes. Because of the small sample size there was considerable uncertainty in the confidence of the estimates (Table 6.5). Fledglings (0-1 years) had the lowest survival estimates (57.14%) followed by 3-5 year old birds with survival estimates of between 57.89%-61.29% (Table 6.5).

Table 6.5. Age specific survival rates (mean \pm standard deviation) expressed as percentages for the Bearded Vulture in southern Africa.

Age Class	Years of data	Survival rate
Fledgling (0-1 year)	2.33	57.14% \pm 38.18%
Juvenile (1-2 years)	11.75	91.49% \pm 37.48%
Immature (2-3 years)	12.00	75.00% \pm 42.14%
Immature (3-4 years)	4.75	57.89% \pm 47.05%
Sub-adult (4-5 years)	2.75	61.29% \pm 41.57%
Sub-adult (5-6 years)	1.83	100.00% \pm n/a
Adult (6-7 & >7 years)	14.58	86.29% \pm 30.70%

Population Growth Rate

Our initial population model (using current survival and productivity estimates) failed to recapitulate the observed population trajectory between 1960 and 2000. Our model predicted a greater decline over those 40 years than was observed, with a predicted current population size of only 1.3 ± 0.4 rather than the 368-408 currently present (Figure 6.4). However, had the population instead consistently experienced the productivity and survival rates estimated by Brown in the late 1980s (Brown 1997), the population would be predicted to be far larger (848 ± 6) than we currently find. The failure of our model to recapitulate the observed population trajectory may also be as a result of the accuracy of Brown's (1997) survival estimates which were based his population estimate of 204 pairs, the breeding success rate of 0.89 young/pair/year, and the numbers of young and sub-adult birds in the population, assuming that the adult population was stable and that recruitment from the

immature population equalled the annual adult mortality. Our models, however, still suggest that there has been a gradual decline in productivity and/or survival during the 1960-2000 period.

Two alternative scenarios were modelled to determine whether reduced productivity or increased mortality could independently account for the historic (1960-2000) decline (Figure 6.4). Modelling historic productivity with current survival resulted in a mean population size of 10 ± 3 after 40 years. By contrast, the scenario based on current productivity and historical survival estimates resulted in a much larger mean population size (590 ± 9) after 40 years. These results suggest that the current survival estimates are more than sufficient to have driven the decline and that a decline in productivity only is unlikely to be fully responsible for the trends observed (Figure 6.4).

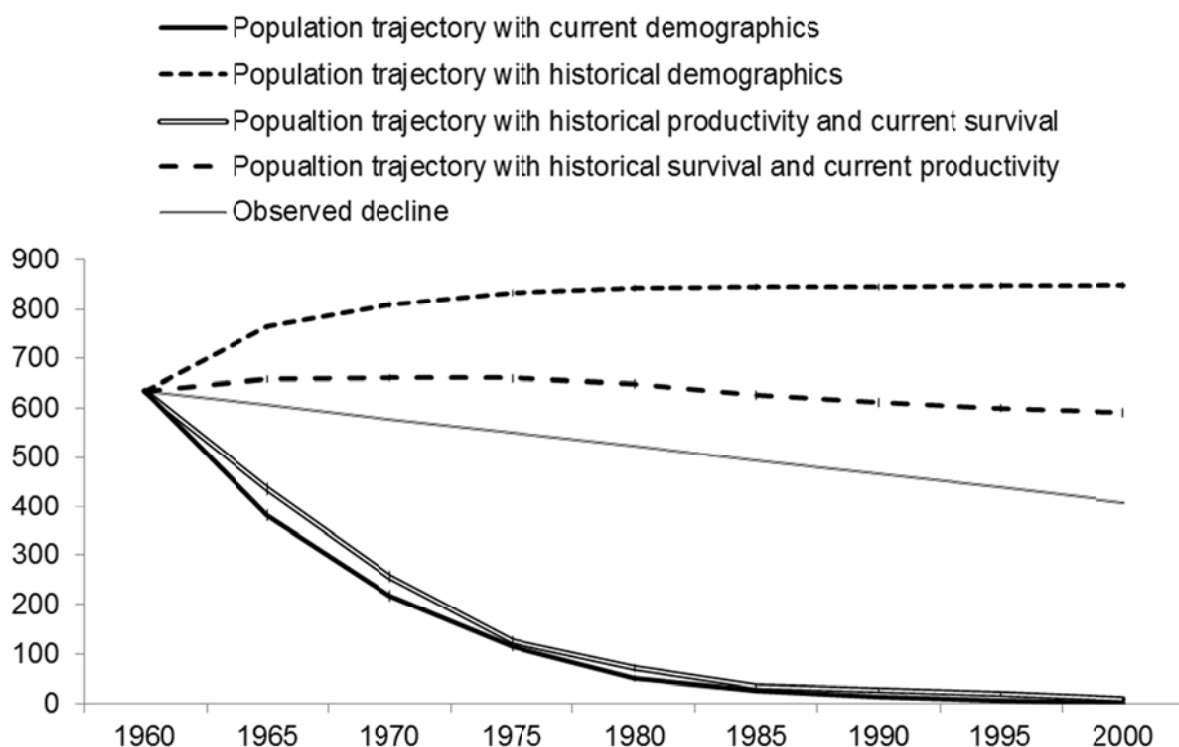


Figure 6.4 Graphical output for the VORTEX simulated population change between 1960 and 2000 comparing observed and modelled trajectories based on the population of 633 individuals i) experiencing current survival and productivity estimates from the start (-), ii) historical survival and productivity estimates from Brown (1997) (...), iii) historical survival and current productivity estimates (--), and iv) historical productivity and current survival estimates (=). Lines show the mean population size (mean \pm SE) at five year intervals for 1000 simulations run for each model over a 40 year period.

Trajectories over a 50 year period from 2000-2050, using the maximum current population estimate ($n=408$), and productivity and demography estimates from this study, resulted in a mean future population size of only 2 ± 1 individuals with a growth rate of $\lambda=0.91$, a 0.99 probability of extinction and a mean time to extinction of 12.24 ± 0.29 years (Figure 6.5). This projection suggests that even after only 10 years, the mean population size would decline to only 143 ± 8 . However, based on the known level of decline that has occurred over the last 10 years, this decline is unrealistically high. For example, the number of abandoned nests during this time (2000-2010) is 11 (S. Krüger *unpubl. data*) and we would estimate that the population should have totalled *ca.* 372 individuals in 2010 (*i.e.* more than twice that predicted by this model). The most likely reason for this is that our survival estimates were too low; and the small sample size used for the calculation of survival rates resulted in large confidence limits around these estimates reinforcing this notion. Therefore for future scenario modelling we adjusted our survival rates so that our models more closely matched the known decline that had occurred over the last 10 years. Thus, we adjusted our survival estimates (increasing them by 40%- see Appendix 6.1)

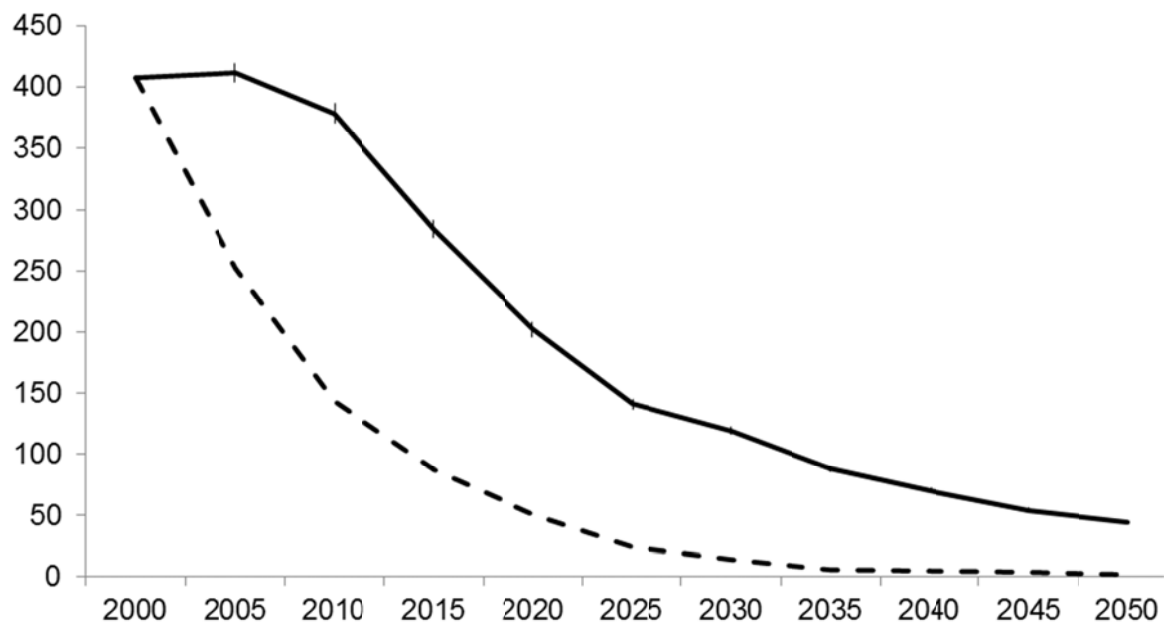


Figure 6.5 Graphical output for the VORTEX projected population change between 2000 and 2050 showing the original projection (---) based on current demographic data and the projection with adjusted mortality rates (-). The mean population size (mean \pm SE) is shown at five year intervals for 1000 simulations run over a 50 year period.

Based on the maximum population number and the adjusted mortality rates and current productivity, trajectories over 50 years from 2000 resulted in a mean population size of 46 ± 6 individuals in 2050 with a $\lambda=0.99$ and a 0.89 probability of extinction and a mean time to extinction of 18.74 ± 0.41 years (Figure 6.5).

Several management interventions were modelled to determine which actions would increase growth rate and reduce the probability of extinction into the future (Tables 6.6 a&b). These interventions included increasing the productivity in 5% intervals and reducing mortality in 10% intervals across all ages (Table 6.6a). We then included the scenario of supplementation of four first year birds (two males and two females) annually for 20 years which we considered practical given the limited resources available currently (Table 6.6b). We considered the minimum management target to be a positive growth rate (*i.e.* $\lambda \geq 1$) with a probability of extinction of <0.50 (*i.e.* $<50\%$ chance of the population going extinct). The best result (*i.e.* positive growth rate $\lambda=1.09$ and lowest probability of extinction $PE=0.30$) was achieved if productivity was increased by 20% and mortality was reduced by 50% with the supplementation of four individuals. Although supplementation did not change the growth rate in any scenario, it did lower the population's probability of extinction in all cases and therefore is a worthwhile management scenario to consider. Scenarios where productivity was increased without a change in mortality rates, still resulted in high probabilities of extinction ($PE=0.88$) whereas scenarios of reduced mortality without a change in productivity resulted in lower extinction probabilities ($PE=0.46$). The minimum management action based on the projected growth rate, was a 15% increase in productivity, a 40% reduction of mortality and supplementation with four first year birds.

Unsurprisingly given the life history strategy of the species, reducing mortality thus has a more significant impact on population growth than increasing productivity and, in order to be an effective strategy, mortality must be reduced across all ages by at least 40% in combination with other management options. This reduction in mortality rate represents about a 10% increase in survival rate which we consider to be achievable.

Table 6.6a Projected population growth rate(λ) and the probability of extinction (PE) between 2000 and 2050 based on the implementation of various management scenarios, of increasing productivity (5% increments) and reducing mortality (10% increments). Scenarios with a positive growth rate and PE <0.50 are highlighted in red.

		Baseline	Increased productivity				
			5%	10%	15%	20%	25%
Reduced mortality	Baseline	$\lambda=0.99$,	$\lambda=1.00$	$\lambda=1.008$	$\lambda=1.01$	$\lambda=1.02$	$\lambda=1.03$
		PE=0.88	PE=0.88	PE=0.90	PE=0.88	PE=0.89	PE=0.88
	10%	$\lambda=1.01$	$\lambda=1.02$	$\lambda=1.02$	$\lambda=1.03$	$\lambda=1.03$	$\lambda=1.04$
		PE=0.88	PE=0.85	PE=0.82	PE=0.80	PE=0.83	PE=0.82
	20%	$\lambda=1.02$	$\lambda=1.03$	$\lambda=1.04$	$\lambda=1.04$	$\lambda=1.05$	$\lambda=1.05$
		PE=0.77	PE=0.76	PE=0.78	PE=0.77	PE=0.79	PE=0.75
	30%	$\lambda=1.04$	$\lambda=1.04$	$\lambda=1.05$	$\lambda=1.06$	$\lambda=1.06$	$\lambda=1.07$
		PE=0.69	PE=0.66	PE=0.68	PE=0.70	PE=0.69	PE=0.67
	40%	$\lambda=1.05$	$\lambda=1.05$	$\lambda=1.06$	$\lambda=1.07$	$\lambda=1.07$	$\lambda=1.08$
		PE=0.57	PE=0.60	PE=0.59	PE=0.60	PE=0.59	PE=0.61
	50%	$\lambda=1.06$	$\lambda=1.07$	$\lambda=1.08$	$\lambda=1.08$	$\lambda=1.09$	$\lambda=1.10$
		PE=0.46	PE=0.49	PE=0.47	PE=0.48	PE=0.47	PE=0.48

Table 6.6b Projected population growth rate(λ) and the probability of extinction (PE) between 2000 and 2050 based on the implementation of various management scenarios, of increasing productivity (5% increments) and reducing mortality (10% increments) with supplementation of the population by two males and females annually for 20 years throughout. Scenarios with a positive growth rate and PE <0.50 are highlighted in red.

		Baseline	Increased productivity				
			5%	10%	15%	20%	25%
Reduced mortality	Baseline	$\lambda=0.99$	$\lambda=1.00$	$\lambda=1.01$	$\lambda=1.01$	$\lambda=1.01$	$\lambda=1.03$
		PE=0.76	PE=0.77	PE=0.78	PE=0.78	PE=0.77	PE=0.73
	10%	$\lambda=1.01$	$\lambda=1.02$	$\lambda=1.02$	$\lambda=1.03$	$\lambda=1.03$	$\lambda=1.04$
		PE=0.74	PE=0.67	PE=0.69	PE=0.69	PE=0.67	PE=0.72
	20%	$\lambda=1.02$	$\lambda=1.03$	$\lambda=1.04$	$\lambda=1.04$	$\lambda=1.05$	$\lambda=1.05$
		PE=0.61	PE=0.63	PE=0.62	PE=0.61	PE=0.61	PE=0.59
	30%	$\lambda=1.04$	$\lambda=1.04$	$\lambda=1.05$	$\lambda=1.06$	$\lambda=1.06$	$\lambda=1.07$
		PE=0.52	PE=0.54	PE=0.54	PE=0.54	PE=0.54	PE=0.53
	40%	$\lambda=1.05$	$\lambda=1.05$	$\lambda=1.06$	$\lambda=1.07$	$\lambda=1.07$	$\lambda=1.08$
		PE=0.45	PE=0.47	PE=0.46	PE=0.43	PE=0.45	PE=0.45
	50%	$\lambda=1.06$	$\lambda=1.07$	$\lambda=1.08$	$\lambda=1.08$	$\lambda=1.09$	$\lambda=1.10$
		PE=0.36	PE=0.34	PE=0.31	PE=0.34	PE=0.30	PE=0.33

Discussion

The main conclusions of this study are four fold. Firstly, the current overall age structure appears to be similar to that found during the early 1980s (Brown 1997), with around a 60/40 split between adults and non-adults. Secondly, productivity in terms of the number of young fledged in occupied territories is relative low and appears to have declined since the early 1980s. Thirdly, survival rates of adults and non-adults appear to be relatively low, with main cause of mortality being due to poisoning, both by pesticides (carbamate insecticides) and lead. Lastly, combining current productivity and survival rates into a population model predicted a continued population decline with a probability of extinction over the next 50 years of 99%. The projected growth rate indicates that the population will not be able to cope with stochastic fluctuations and that immediate action is necessary to mitigate the threats and improve the long-term situation for the species.

Our models showed that reduced productivity alone was insufficient to explain the overall levels of decline witnessed over recent decades, and suggest that this reduction combined with a decrease in survival rate must be responsible. Similar analyses carried out on the vulture population declines in South Asia also highlighted a reduction in productivity alone was insufficient to account for the catastrophic decline of the *Gyps* vulture populations in Pakistan (Sarrazin *et al.* 2004). Adult survival rate is the primary demographic factor influencing the rate of population increase in large raptors (Newton 1979, Lebreton and Clobert 1991). Our study showed unusually high adult mortality rates from marked birds (14%), and a high overall percentage of adults found dead during the study period (21%), relative to those of other large raptors that have mortality rates of between 3-9 % (Sherrod *et al.* 1977, Watson 1990, Whitfield *et al.* 2004, Evans *et al.* 2009, Schaub *et al.* 2009). We have shown that adult mortality has doubled since Brown's (1997) estimates in the 1980s but the population age structure has not changed much over time. This therefore suggests that mortality rates may have increased in all age classes equally with a negative effect on the population growth.

In order to meet the objectives in the Biodiversity Management Plan for the species in southern Africa (Krüger 2013), conservation measures to halt the projected decline and ensure a positive growth rate must be implemented. Although reducing adult mortality should be the primary focus of any management intervention, we recognise that interventions are unlikely to target age-specific segments of the population, and there is a need to reduce mortality across all age classes. Our models have shown that a positive population growth rate with an acceptable probability of extinction can be achieved by reducing mortality by 40% rate across all age groups in combination with increasing productivity by 15% and supplementing the population. The causes of mortality identified in this study suggest that poisoning is still the primary mortality factor affecting this population with power line collisions contributing to more mortalities than originally thought. A power line mitigation strategy is in place through a partnership between Eskom (the electricity utility in South Africa) and the Endangered Wildlife Trust (van Rooyen and Smallie 2006). This partnership is also engaging with the Electricity Corporation in Lesotho (LEC) to reduce bird collisions and electrocutions. The strategy, however, is a reactive one and as such there is an opportunity for the implementation of a project to identify power lines in high use areas and prioritise these for mitigation. This project could follow the methods of Reid *et al.*'s (*in review*) spatial analyses of Bearded Vulture movements in southern Africa to inform wind turbine placement. Since poisoning is the primary mortality factor we suggest that interventions should focus on a reduction in poisoning and to a lesser extent on mitigating power line collisions. A multi-pronged strategy is required to address the impacts of poisoning throughout the species' range by directing attention to the causes of poisoning. In Lesotho, conservation efforts need to focus on addressing the direct poisoning of vultures for the traditional medicine trade (Beilis and Esterhuizen 2005) and by herders that believe vultures are a threat to livestock (S. Zwakala *unpubl. data*). Suggested conservation measures include using District Environmental Officers to engage with traditional healers and herders and educating scholars and range management associations on the importance of vultures and engaging with law enforcement officials to prosecute those killing vultures and illegally

trading in vulture parts. In South Africa, vultures are the indirect targets of predator poison baits (Brown 1991, Krüger *et al.* 2006) and conservation efforts must focus on i) exploring alternative, effective and legal predator control measures (such as the use of guard animals), ii) regulating the import, manufacture and use of agricultural chemicals and pharmaceutical products known to be lethal to vultures and iii) stringent law enforcement measures to prosecute and impose harsh penalties on perpetrators of poisoning.

Our study has also demonstrated a new threat to the population in the form of lead accumulation in bones, suggesting that the birds are ingesting carcasses containing lead shot or bullet fragments (Mateo *et al.* 1999, Clark and Scheuhammer 2003) or ingesting lead in other ways such as through preening feathers after bathing in soil contaminated with lead (A. Llopis *pers. comm.*). Lead is a highly toxic heavy metal and lead poisoning is the most common type of heavy metal poisoning in raptors (Franson 1996, Pain *et al.* 2005), and even at concentrations below those known to cause acute death, individuals experience increased susceptibility to diseases and accidents (Clark and Scheuhammer 2003, Pain *et al.* 2007). Long lived species in particular are very susceptible to the bioaccumulation of lead in bone tissue (Gangoso *et al.* 2009) and the long term effects of lead poisoning have been relevant in the decline of threatened populations such as the California Condor (*Gymnogyps californianus*) (Cade 2007, Hall *et al.* 2007, Green *et al.* 2008) and other long lived raptors worldwide (Kenntner *et al.* 2001, Clark and Scheuhammer 2003, Pain *et al.* 2005, Hernández and Margalida 2009). We advocate the banning of hunting and culling with lead ammunition in the distribution range of the species as suggested by Hernández and Margalida (2009), an approach which has been shown by Cade (2007) and Ancora *et al.* (2008) to be successful in reducing the prevalence of lead exposure. Management strategies must be put in place to enforce this ban; e.g. provision of lead-free ammunition and raising awareness amongst hunters and farmers on the effects of lead on both human and wildlife populations. The primary source of lead from ammunition is assumed to be from animals shot and placed at feeding sites since hunting and culling of wild ungulates in protected areas occur at a low intensity throughout the species' range.

Although high mortality rates have been recorded for this population relative to other raptors, lowered productivity is likely to be a contributing factor to the decline documented for this population. The nesting success of the Bearded Vulture in southern Africa, although not as high as recorded by Brown (1997), is still higher than recorded in most other studies of the species. However, the birds do not attempt to breed as frequently as recorded in the past thereby lowering the overall productivity of the population. The productivity recorded for the southern African population (0.55 y/pr/yr) is within the range of nesting success rates recorded globally for the species; 0.55 y/pr/yr recorded for East Africa (Brown 1977) and Ethiopia (Brown *et al* 1982); 0.66 y/pr/yr for the French Pyrenees (Terasse 1991) and between 0.43 and 0.65 y/pr/yr in the Spanish Pyrenees (Heredia 1991; Margalida *et al* 2003). Our results are also comparable with those of other large raptors (for example; Brown and Hopcroft 1973; Gargett 1977; Mundy 1982; Vernon, Piper and Schultz 1983; Tarboton and Allan 1984; Watson 1990).

Our study found no differences in productivity between nests located in the core or the periphery of the range. Results from Chapter 3 show that the densities of power lines and settlements had the greatest influence on territory occupancy regardless of their location in the range. In Chapter 3, settlement density was used as a surrogate for poisoning, and in this chapter we found poisoning and power line collisions to be the primary causes of mortality. Our models showed that efforts to increase productivity alone will not have the desired effect on population growth but coupled with a reduction in mortality rates and supplementation, a positive growth rate could be achieved. Apart from reducing the levels of disturbance (such as mountaineering or flying) near nest sites, measures to improve the laying rate in adults and first year bird survival need to be identified and implemented. Food availability is a major factor influencing egg laying for many raptors (Steenhof *et al.* 1997, Newton 2002) therefore we speculate that supplementary feeding may increase the laying rate. To be effective feeding must be implemented *before* the egg laying period since Margalida (2010) found supplementary feeding during the chick rearing period in the Spanish Pyrenees to be ineffective in increasing nesting success or individual breeding

performance of territories. Feeding sites must also be appropriately sited since Carrete *et al.* (2006) found supplementary feeding to be one of the main causes of productivity decline, due to an aggregation of non-breeding birds leading to agonistic encounters and interference with the breeding pairs. Feeding sites must also be well managed to reduce incidences of indirect poisoning from lead or harmful veterinary drugs (Anderson, Piper and Swan 2005). Further research is required on factors influencing laying rate and nesting success in order to implement measures to improve the population's productivity.

The release of fledglings as part of a reintroduction or population supplementation programme has been a successful strategy executed for raptor populations in Europe (see for example Green *et al.* 1996, Evans *et al.* 2009) and to re-establish Bearded Vulture populations within their former range (Hirzel *et al.* 2004; Schaub *et al.* 2009). Since reintroduction programmes are costly and time intensive, it is important to establish whether they are feasible and necessary and for this reason we included this scenario in our models. Our models suggest that this management strategy will reduce the probability of population extinction if combined with reduced mortality and increased productivity. We therefore recommend captive breeding (or second egg removal) as a precaution to ensure the long-term survival of this threatened species and to provide a stock of birds for future reintroduction programmes. Supplementation through reintroductions from another population may assist by increasing the genetic diversity of the population.

Declining populations often exhibit a loss of genetic diversity, particularly if exchange with other populations is minimal (Richards 2000). Reduced diversity may decrease fitness or limit the long term capacity of the population to respond to environmental challenges or chance environmental or demographic events in the short term and thus affecting survival and reproduction (Alexandre *et al.* 2007). A recent genetic study using Mitochondrial control region analyses detected reduced haplotype diversity in southern Africa (Krüger *et al.* 2014b, Chapter 5) therefore apart from the known environmental threats to Bearded Vultures in southern Africa, genetic diversity is already considerably reduced. Sustained declines are

the main reason for loss of genetic diversity therefore for the long term persistence of the Bearded Vulture in southern Africa it is essential to maintain an adequate population size and high levels of genetic diversity. The management option of introducing individuals from Ethiopia which are genetically closely related to the southern African population (Krüger *et al.* 2014b, Chapter 5) or using these individuals in a captive breeding programme should be considered.

Recent information on the population dynamics of the southern Africa Bearded Vulture has allowed us to model the population trends more accurately which together with the knowledge of the primary causes of mortality provide the necessary details to target management actions more effectively through the interventions suggested above. The threat of poisoning has not been addressed over the past few decades and if this trend continues, the population faces the risk of extinction within the next few decades. Many scavenger populations are facing the same threats and we urge authorities to unite in the fight against the illegal use of poison on a continent wide scale as the best use of limited resources. Our results may form an important baseline for future studies in the area or elsewhere in Africa where vultures are undergoing rapid declines.

Acknowledgements

Numerous Ezemvelo KwaZulu-Natal Wildlife Staff and Bearded Vulture Task Force members assisted with breeding territory surveys in South Africa and Lesotho. Shane Elliott, Chris Brown, John Crowson and Rickert van der Westhuizen are thanked for their assistance with vehicle surveys. Ian Rushworth assisted with the baseline model for the PVA. A number of individuals are thanked for the recovery of marked birds, often under challenging circumstances, in particular; Makhubu Shobana, Tanya Smith, Henry Hlela and Rickert van der Westhuizen. Dr. Voster from Vet Diagnostix is thanked for his voluntary assistance with post mortems.

References

- Alexandre R, Couvet D and Sarrazin F (2007) Integration of demography and genetics in population restorations. *Ecoscience* 14: 463–471. doi:10.2980/1195-6860(2007)14 [463: IODAGI]2.0.CO;2.
- Ancora S, Bianchi N, Leonzio C and Renzoni A. (2008) Heavy metals in flamingos (*Phoenicopterus ruber*) from Italian wetlands: The problem of ingestion of lead shot. *Environ Res* 107(2): 229-236.
- Anderson MD, Piper SE and Swan GE (2005) Non-steroidal anti-inflammatory drug use in South Africa and possible effects on vultures. *S Afr J Sci* 101: 1-3.
- Beilis N and Esterhuizen J (2005) The potential impact on Cape Griffon *Gyps coprotheres* populations due to the trade in traditional medicine in Maseru, Lesotho. *Vulture News* 53: 15-19.
- Beissinger S and McCullough D (editors) (2002) Population Viability Analysis. University of Chicago Press, Chicago.
- Boshoff AF, Anderson MD and Borello W (editors) (1998) Vultures in the 21st century. Vulture Study Group, Johannesburg.
- Brown LH (1977) The status, population structure, and breeding dates of the African lammergeier *Gypaetus barbatus meridionalis*. *Raptor Res* 11: 49-58.
- Brown CJ (1991) An investigation into the decline of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Biol Conserv* 57(3): 315-337.
- Brown CJ (1992) Distribution and status of the bearded vulture *Gypaetus barbatus* in southern Africa. *Ostrich* 63(1): 1-9.
- Brown CJ (1997) Population dynamics of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Afri J Ecol* 35(1): 53-63.

- Brown JH (1971) Mammals on mountaintops: nonequilibrium insular biogeography. *Am Nat* 105: 467–478.
- Brown JH (1995) Macroecology. Chicago University Press, Chicago.
- Brown LH, Urban EK and Newman K (1982) Birds of Africa. Vol. 1. Academic Press, Orlando, Florida.
- Brown LH and Hopcroft JBD (1973) Population structure and dynamics of the African fish eagle *Haliaeetus vocifer* (Daudin) at Lake Naivasha, Kenya. *E Afr Wildl J* 11: 255–269.
- Cade TJ (2007) Exposure of California Condors to lead from spent ammunition. *J Wildl Manage* 71(7): 2125–2133.
- Carrete M, Donázar JA and Margalida A (2006) Density-dependent Productivity Depression in Pyrenean Bearded Vultures: Implications for Conservation. *Ecol Appl* 16(5): 1674–1682.
- Clark AJ and Scheuhammer AM (2003) Lead poisoning in upland-foraging birds of prey in Canada. *Ecotoxicology* 12: 23–30.
- Diamond JM, Bishop KD and van Balen S (1987) Bird survival in an isolated Javan woodland: Island or mirror? *Conserv Biol* 2: 132–142.
- Energy Sector Policy of the AfDB Group (2012) African Development Bank Operational Resources and Policies Department (ORPC).
- Evans RJ, Wilson JD, Amar A., Douse A., MacLennan A, Ratcliffe N and Whitfield DP (2009) Growth and Demography of a re-introduced population of White-tailed Eagles *Haliaeetus albicilla*. *Ibis* 151: 244–254
- Ferrer M, Newton I, Muriel R, Báguena G, Bustamante J, Martini M and Morandini V (2014) Using manipulation of density-dependent fecundity to recover an endangered

- species: the bearded vulture *Gypaetus barbatus* as an example. *J Appl Ecol* July 2014. doi: 10.1111/1365-2664.12308
- Foufopoulos J and Ives AR (1999) Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. *Am Nat* 153: 1–25.
- Franson JC (1996) Interpretation of tissue lead residues in birds other than waterfowl. In: Beyer WN, Heinz GH and Redmon-Norwood AW (editors) *Environmental Contaminants in Wildlife: Interpreting Tissue Concentrations*. SETAC, CRC Lewis Publishers, Boca Raton, FL, pp. 265–279.
- Gangoso L, Ivarez-Lloret PA, Rodríguez-Navarro AAB, Mateo R, Hiraldo F and Donázar JA (2009) Long-term effects of lead poisoning on bone mineralization in vultures exposed to ammunition sources. *Environ Pollut* 157: 569–574.
- Gargett V (1977) A 13 year population study of the black eagles in the Matopos, Rhodesia, 1964-1976. *Ostrich* 48: 17-27.
- Gaston KJ (1994) *Rarity*. Chapman and Hall, London.
- Gilpin ME and Soulè ME (1986) Minimum viable population: proceses of species extinctions. In: Soulè ME (editor) *Conservation Biology: the Science of Scarcity and Diversity*. Sinauer, Sunderland, Massachusetts, pp. 19-34.
- González LM, Margalida A, Mañosa S, Sánchez R, Oria J, Molina JI, Caldera J, Aranda A and Prada L (2007) Causes and spatio-temporal variations of non-natural mortality in the Vulnerable Spanish imperial eagle *Aquila adalberti* during a recovery period. *Oryx* 41: 495–502.
- Green RE, Pienkowski MW and Love JA (1996) Long-term viability of the re-introduced population of the White-tailed Eagle *Haliaeetus albicilla* in Scotland. *J Appl Ecol* 33: 357–368.

- Green RE, Hunt WG, Parish CN and Newton I (2008) Effectiveness of action to reduce exposure of free-ranging California condors in Arizona and Utah to lead from spent ammunition. *PLoS ONE* 3(12): e4022.
- Hall M, Grantham J, Posey R and Mee A (2007). Lead exposure among reintroduced California Condors in southern California. *California Condors in the 21st Century*, 139-162.
- Hernández M and Margalida A (2009) Assessing the risk of lead exposure for the conservation of the endangered Pyrenean bearded vulture (*Gypaetus barbatus*) population. *Environ Res* 109: 837–842.
- Heredia R (1991) Chapter 2. Biología de la Reproducción. In: Heredia R and Heredia B (editors). *El Quebrantahuesos (Gypaetus barbatus) en los Pirineos*. ICONA, Madrid.
- Hiltunen TA (2008) Farmers and the Bearded Vulture *Gypaetus barbatus meridionalis*. Dissertation, University of Pretoria.
- Hirzel AH, Posse B, Oggier P, Crettenand Y, Glenz C and Arlettaz R (2004) Ecological requirements of reintroduced species and the implications for release policy: the case of the bearded vulture. *J Appl Ecol* 41: 1103–1116.
- IUCN (2001) IUCN Red List Categories and Criteria: version 3.1. IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK. ii + 30pp.
- Jones HL and Diamond JM (1976) Short-time base studies of turnover in breeding birds of the California Channel Islands. *Condor* 76: 526–549.
- Kalipeni E (editor) (1994) Population Growth and Environmental Degradation in Africa, 236 pp.

- Kenntner N, Tataruch F and Krone O (2001) Heavy metals in soft tissue of white-tailed eagles found dead or moribund in Germany and Austria from 1993 to 2000. *Environ Toxicol Chem* 20: 1831–1837.
- Krüger S (editor) (2013) Biodiversity Management Plan for the Bearded Vulture (*Gypaetus barbatus meridionalis*) for Southern Africa, *unpubl report*.
- Krüger S (*in press*) Bearded Vulture. In: Taylor MR (editor) The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. BirdLife South Africa, Johannesburg.
- Krüger S, Piper S, Rushworth I, Botha A, Daly B, Allan D, Jenkins A, Burden D and Friedmann Y (editors.) (2006) Bearded Vulture (*Gypaetus barbatus meridionalis*) Population and Habitat Viability Assessment Workshop Report. Conservation Breeding Specialist Group (SSC/IUCN)/CBSG Southern Africa. Endangered Wildlife Trust, Johannesburg.
- Krüger SC, Allan DG, Jenkins AR and Amar A (2014a) Trends in territory occupancy, distribution and density of the Bearded Vulture *Gypaetus barbatus meridionalis* in southern Africa. *Bird Conserv Int* 24: 162-177. doi:10.1017/ S0959270913000440.
- Krüger SC, Wesche PL and Jansen van Vuuren B (2014b) Reduced genetic diversity in Bearded Vultures *Gypaetus barbatus* in Southern Africa. doi: 10.1111/ibi.12200.
- Lacy RC, Borbat M and Pollak JP (2005) VORTEX: A Stochastic Simulation of the Extinction Process. Version 9.50. Brookfield, IL: Chicago Zoological Society.
- Lande R (1999) Extinction risks from anthropogenic, ecological and genetic factors. In: Landweber F and Dobson AP (editors.) Genetics and the extinction of species. Princeton University Press, pp. 1-22.
- Lebreton J-D and Clobert J (1991) Bird population dynamics, management, and conservation: the role of mathematical modelling. In: Perrins CM, Lebreton J-D and

- Hirons GJM (editors) Bird population studies: relevance to conservation and management. Oxford University Press, Oxford, pp. 105-125.
- MacArthur RH and Wilson EO (1967) The equilibrium theory of island biogeography. Princeton University Press, Princeton.
- Mander M, Diederichs N, Ntuli L, Khulile M, Williams V and McKean S (2007) Survey of the Trade in Vultures for the Traditional Health Industry in South Africa. Futureworks, *unpubl report*, 30pp.
- Margalida A (2010) Supplementary feeding during the chick-rearing period is ineffective in increasing the breeding success in the bearded vulture (*Gypaetus barbatus*). *Eur J Wildl Res* 56: 673–678.
- Margalida A, Canut J and García D (2003) Territory change and Nest-site switching in the Bearded Vulture (*Gypaetus barbatus*). *J Raptor Res* 37(4): 333-337.
- Margalida A, Heredia R, Razin M and Hernandez M (2008) Sources of variation in mortality of the Bearded Vulture *Gypaetus barbatus* in Europe. *Bird Conserv Int* 18: 1-10.
- Margalida A, Oro D, Cortés-Avizanda A, Heredia R, Donazar JA (2011) Misleading Population Estimates: Biases and Consistency of Visual Surveys and Matrix Modelling in the Endangered Bearded Vulture. *PLoS ONE* 6(10): e26784. doi:10.1371/journal.pone.0026784
- Mateo R, Estrada J, Paquet JY, Riera X, Domínguez L, Guitart R and Martínez-Vilalta A (1999) Lead ingestion by marsh harriers *Circus aeruginosus* from the Ebro Delta, Spain. *Environ Pollut* 104: 435–440.
- Mateo-Tomás P and Olea PP (2010) Diagnosing the causes of territory abandonment by the Endangered Egyptian vulture *Neophron percnopterus*: the importance of traditional pastoralism and regional conservation. *Oryx* 44: 424–433.

- Mundy PJ (1982) The Comparative Biology of Southern African Vultures. Vulture Study Group, Johannesburg.
- Newton I (1979) Population Ecology of Raptors. T and AD Poyser, Berkhamsted.
- Newton I (1998) Population Limitation in Birds. Academic Press, London.
- Newton I (2002) Population limitation in Holarctic owls. In: Newton I, Kavanagh R, Olsen J and Taylor I (editors) Ecology and conservation of owls. CSIRO Publishing, Collingwood, Victoria, Australia, pp 3–29.
- Ngwenya NP (2001) Implications of the medicinal animal trade for Nature Conservation in KwaZulu-Natal. Ezemvelo KZN Wildlife *unpubl report*, 76pp.
- Ogada DL, Keesing F and Virani MZ (2012) Dropping dead. Causes and consequences of vulture population declines worldwide. *Ann NY Acad Sci* 1249: 57-71.
- Pain DJ, Metayer C and Amiard JC (1993) Lead determination in avian blood: application to a study of lead contamination in raptors from France. *J Environ Anal Chem* 53: 29–35.
- Pain DJ, Meharg AA, Ferrer M, Taggart M and Penteriani V (2005) Lead concentration in bones and feathers of the globally threatened Spanish imperial eagle. *Biol Conserv* 121: 603–619.
- Pain DJ, Carter I, Sainsbury AW, Shore RF, Eden P, Taggart MA, Konstantinos S, Walker LA, Meharg AA and Raab A (2007) Lead contamination and associated disease in captive and reintroduced red kites *Milvus milvus* in England. *Sci Tot Environ* 376: 116–127.
- Penzhorn BL (1969) Golden Gate se Lammergeiers. *Afr Wildl* 23: 289-298.
- Pimm SL, Diamond J, Reed TM, Russell GJ and Verner J (1993) Times to extinction for small populations of large birds. *Proc Nat Acad Sci USA* 90: 10871–10875.

- R Core Team. (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org>.
- Reid T, Krüger S, Whitfield P and Amar A (*in review*). Spatial analyses of Bearded Vulture movements in southern Africa to inform wind turbine placement.
- Richards CM (2000). Inbreeding depression and genetic rescue in a plant metapopulation. *Am Nat* 155: 625-640.
- Rosenzweig ML (1995) Species Diversity in Space and Time. Cambridge University Press, Cambridge.
- Saether B and Bakke Ø (2000) Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81: 642–653.
- Sarrazin F, Virani MZ, Gilbert M and Khan A (2004) Preliminary Population Viability Analyses for Oriental White-Backed Vulture *Gyps bengalensis* in Punjab province, Pakistan. In: Chancellor RD and Meyburg BU (editors) Raptors Worldwide. WWGBP & MME Penti Kft, Budapest, pp. 257–262.
- Schaub M and Pradel R (2004) Assessing the relative importance of different sources of mortality from recoveries of marked animals. *Ecology* 85(4): 930-938.
- Schaub M, Zink R, Beissmann H, Sarrazin F and Arlettaz R (2009) When to end releases in reintroduction programmes: demographic rates and population viability analysis of bearded vultures in the Alps. *J Appl Ecol* 46: 92–100. doi: 10.1111/j.1365-2664.2008.01585.x
- Shaffer ML (1981) Minimum population sizes for species conservation. *Biosci* 31: 131-4.
- Sherrod SK, White CM and Williamson FSL (1977) Biology of the bald eagle (*Haliaeetus leucocephalus alascanus*) on Amchitka Island, Alaska. *Living Bird* 15: 143–182.

- Soulé ME, Bolger DT, Alberts AC, Wright J, Sorice M and Hill S (1988) Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv Biol* 2: 75–92.
- Smart J, Amar A, Sim IMW, Etheridge B, Cameron D and Christie G (2010) Illegal killing slows population recovery of a re-introduced raptor of high conservation concern – The red kite *Milvus milvus*. *Biol Conserv* 143: 1278–1286.
- Steenhof K, Kochert MN and McDonald TL (1997) Interactive effects of prey and weather on golden eagle reproduction. *J Anim Ecol* 66(3): 350-362.
- Steenhof K and Newton I (2007) Assessing nesting success and productivity. In: Bird DM and Bildstein KL (editors) Raptor research and management techniques. Hancock House Publishers, Surrey, British Columbia, Canada, pp. 181–192.
- Tarboton WR and Allan DG (1984) The Status and Conservation of Birds of Prey in the Transvaal. *Transvaal Mus Monogr* 3, Transvaal Museum, Pretoria.
- Terasse JF (1991) Chapter 11. Le Gypaete Barbu dans les Pyrénées Françaises. In: Heredia R and Heredia B (editors) El Quebrantahuesos (*Gypaetus barbatus*) en los Pirineos. ICONA, Madrid.
- van Rooyen CS and Smallie J (2006) The Eskom – Endangered Wildlife Trust Strategic Partnership in South Africa: A brief summary. *Nature and Fauna* 21(1): 25.
- Vernon CJ, Piper SE and Schultz DM (1983) The Cape vulture at Colleywobblers, Transkei in 1982. *Vulture news* 9/10: 11-13.
- Watson RT (1990) Population dynamics of the bateleur in the Kruger National Park. *Ostrich* 61: 5-12.
- Whitfield DP, Fielding AH, Mcleod DRA and Haworth PF (2004) Modelling the effects of persecution on the population dynamics of golden eagles in Scotland. *Biol Conserv* 119: 319–333.

Appendices

Appendix 6.1 Summary of baseline parameter values used in Vortex for the simulations of the observed population trajectory for the past 40 years (based on data from Brown (1997) and data from this chapter) and future trajectories modelled over the next 50 years (based on data from this chapter and Krüger *et al.* (2014a, Chapter 2).

Parameter	Value	
	Past 1960-2000	Future 2000-2050
Number of iterations	1000	1000
Number of years	50	50
Extinction definition	One sex remains	One sex remains
Number of populations	One	One
Initial population size (N)	633	408
Carrying capacity (K)	1000 \pm 10	1000 \pm 10
Age distribution	Stable	Stable
Inbreeding depression	No	No
Density dependent reproduction	No	No
EV concordance of reproduction and survival	Yes	Yes
Mating system	Long-term monogamy	Long-term monogamy
Age of first breeding	7	7
Maximum age of reproduction	32	32
Maximum number of broods per year	1	1
Maximum progeny per brood	1	1
Sex ratio at birth	50%	50%
Percent adult females breeding	100% \pm 10%	72% \pm 20%
Fecundity rate	0.89	0.76
Number of offspring per female per brood	1 \pm 0	1 \pm 0
Percentage adult males in the breeding pool	100%	98%
Mortality Rates (percentage) years	0-1	25.80 \pm 38.18
	1-2	05.40 \pm 37.48
	2-3	15.00 \pm 42.14
	3-4	25.20 \pm 47.05
	4-5	22.80 \pm 41.57
	5-6	0
	6-7	08.40 \pm 30.70
	>7	08.40 \pm 30.70
Number of catastrophes	None	None
Harvest	No	No
Supplementation	No	No

Appendix 6.2 The details of the vehicle survey routes undertaken in the Bearded Vulture's range in southern Africa during 2012.

Parameters	Day, month and year of survey		
	(1) 4-6,18&19	(2) 13&14,29&30	(3) 18-20,29&30
	July 2012	September 2012	December 2012
Total distance (km)	816.00	799.00	616.00
Total time (hours)	37.10	26.90	25.40
Total Bearded Vultures per 100 km	0.86	2.00	0.65
Adult Bearded Vultures per 100 km	0.86	1.13	0.00
Non adult Bearded Vultures per 100 km	0.00	0.75	1.64
unknown Bearded Vultures per 100 km	0.00	0.13	4.92
Total Bearded Vultures per 10 hours	1.89	5.95	1.57
Adult Bearded Vultures per 10 hours	1.89	3.35	0.00
Non Adult Bearded Vultures per 10 hours	0.00	2.23	0.39
unknown Bearded Vultures per 10 hours	0.00	0.37	1.18
Total Cape Vultures per 100 km	1.10	2.63	6.17
Total Cape Vultures per 10 hours	2.43	7.81	14.96
Total Ravens per 100 km	4.90	12.89	0.49
Total Ravens per 10 hours	10.80	38.29	1.18

- (1) Western Lesotho routes: between bottom of Sani Pass and Roma via Thaba-Tseka
 (2) Eastern Lesotho: between top of Sani Pass and Butha Buthe via Mokhotlong
 (3) North-eastern Cape: between Mt Fletcher and Karingmelkspruit via Ongeluksnek, Maclear, Naudes Nek, Rhodes, Dangershoek, Balloch, Barkly East, Elliott, Bottlenek Pass and Mosheshe's Ford

Chapter 7: Discussion



Photo 7 Juvenile Bearded Vulture on a Drakensberg cliff

In this thesis I have attempted to synthesize 15 years of research on the Bearded Vulture population of southern Africa to document the current status and distribution and to achieve a better understanding of the factors which may be limiting population growth, their movement ecology and the genetic diversity of the population (Figure 7.1). Results from this thesis have confirmed the urgency for intervention and provided the necessary information to enable conservation action to be focussed most effectively to improve the status of the species. This research is timely in that it can add value to the international strategy for the management of the Bearded Vulture, the African Vulture strategy and the Biodiversity Management Plan for the species locally.

The first task when investigating the decline of a population is to establish baseline information on the population's size and distribution range. This information was lacking for the Bearded Vulture in southern Africa and as such we had no knowledge on how the population had fared over recent years. Therefore it was important to firstly establish the current population size and the extent of its distribution. Chapter 2 achieves this through multiple surveys of breeding territories which confirm the declining trend in the Bearded Vulture population in southern Africa recorded by Brown (1991), Allan and Jenkins (2005), Krüger (2006) and Krüger *et al.* (2006). There was some uncertainty around the exact rate of decline because the historical status of newly discovered territories was unknown and pairs may have moved territories rather than abandoning them. However, Chapter 2 estimated that the breeding population had declined in number (32-51%), range (27%) and density (20%) over the past fifty years, with territories on the edge of the range being more likely to be abandoned than those in the core where breeding densities were higher. Surveys to determine the relative abundance and age structure of the population, confirmed the declining trends based on very low encounter rates (3.14 birds/10 hours) of both adults and non-adults throughout the range, which were 45% lower than recorded 30 years previously. However, although numbers were small, these surveys suggested that there was little change in age structure over the same time period. The extensive surveys conducted across the entire species' range over a period of more than 12 years, resulted in many new

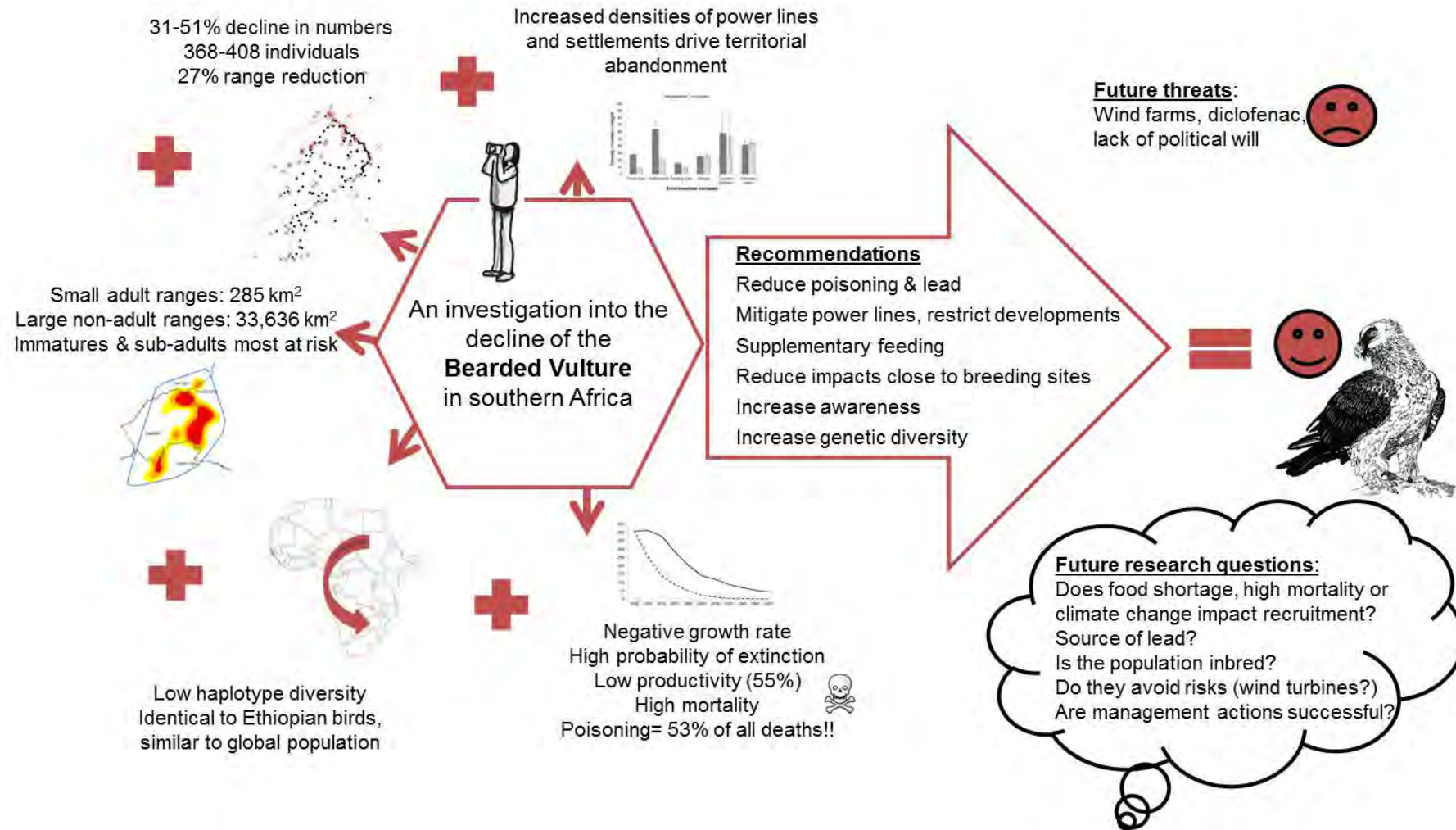


Figure 7.1 Infographic of the main findings, conclusions and management recommendations of the study.

territories being identified, including those that had been unoccupied (considered abandoned) for many years. The southern African population was estimated at 352-390 (Krüger *et al.* 2014a, Chapter 2) based on Brown's (1997) age ratios for the population (1 adult : 0.60 non-adults). The current age ratios established for the population in Chapter 6 (1 adult : 0.67 non-adults) enabled a more accurate estimate of the population to be calculated; that of 368 – 408 individuals.

As a result of the work reported on in Chapter 2, the regional status of the species was uplisted from Endangered (Anderson 2000) to Critically Endangered (Krüger *in press*) in a recent reassessment of the red data bird species of South Africa, Lesotho and Swaziland (Taylor *in press*). This was based on the reduction in population size and geographic range, and the threats to the species not being addressed. These data also contributed to the recent global uplisting of the species from Least Concern to Near Threatened based on a declining trend in many parts of their range attributed to poisoning, disturbance and collisions with power lines (BirdLife International 2014).

Given that many of the identified territories had now become abandoned, and that ultimately it is this abandonment that had resulted in a decline in the population, I was interested in ascertaining what factors might have been driving this abandonment. Such an approach has proven useful in other studies for example Carrete *et al.* (2007) and Mateo-Tomás and Olea (2010). Chapter 2 identified that territories on the periphery of the range were more likely to be abandoned than those in the core range where breeding densities were higher. This finding was thought to possibly result from higher anthropogenic pressures operating at the periphery of the range. I investigated this interaction further in Chapter 3 where I considered three hypotheses proposed as drivers of territorial abandonment; anthropogenic impact, climate change and food availability. These hypotheses were investigated through the use of covariates within the area representing the home-ranges of adults surrounding each territory. Data from Chapter 4 (see below) provided the average home range size of breeding adults – which allowed me to delimit a suitable area over which

to obtain these covariates. Findings from this chapter showed that anthropogenic activities were indeed the most influential factors associated with the abandonment of territories. Further investigations showed that this pattern was not simply the result of the population shrinking back to the core of the range, since territories with higher densities of power lines and settlements were more likely to be abandoned regardless of their location within the range. The results of this chapter hinted at the overall cause of population's decline being as the result of human impacts. Further support for this conclusion was provided by the causes of mortality identified in Chapter 6. The primary mortality factors were poisoning (53% of cause of death) and collisions with power lines (21%) with both causes likely to be under-reported because of the difficulty in finding carcasses in the rugged mountainous terrain and the reluctance of landowners to report carcasses on their properties.

Equipped with the knowledge that human impacts were the probable causes of the population decline, I was then interested to explore which age classes were most at risk of encountering these threats and whether their use of the landscape made them more vulnerable to risk factors. Data from 24 individuals of differing age classes fitted with satellite tags between 2007-2013 provided the necessary information to compare home range size, use and exposure to risks (e.g. settlements and power lines) between age classes in Chapter 4. Although adults are a conservation priority (Newton 1979, Bell and Merton 2002), this chapter revealed that immature and sub-adult age classes experience the highest risk of collisions with power lines and interactions with humans as a result of their larger range sizes and the greater distances they move in relation to the other age classes. The results highlight the importance of focussing conservation efforts on these age classes as well as on adults. Examining the geographical areas used by non-adults provides conservation authorities with three options in terms of the size of the area (50%, 75% and 90% kernel areas) in which to focus conservation activities targeting these age classes, depending on the availability of resources. The core area of use by non-adults (10,982 km²) represents the minimum sized area in which to implement the recommendations listed below. Since adults focus their activities within a relatively small area around their nest sites (ca. 10 km radius)

and move almost exclusively in this area (92% of all fixes), breeding territories should form the minimum area of focus for conservation actions (e.g. power line mitigations and educational activities). Adult home range areas (including breeding and non-breeding birds) in southern Africa were similar to those recorded in Europe but the home range of birds which were breeding was only a third of the size. Non-adults ranged over much larger areas than recorded elsewhere, in fact they used 65% of the area occupied by the species, thus presenting a challenge for the implementation of conservation actions across regional and international boundaries.

The capture of 24 individuals (Chapter 4) provided me with an opportunity to collect tissue samples for genetic analyses. I was interested to know how genetically similar the southern African population was to the Ethiopian population and other populations globally. Previous research had shown that there was no distinction between the populations globally (Godoy *et al.* 2004), but the small number of samples from sub-Saharan Africa made me cautious of these findings. Knowing the population's diversity and evolutionary placement will aid decisions on whether introductions are necessary to increase numbers and diversity and where best to source individuals from. The genetic variation in the population discussed in Chapter 5 showed that apart from the anthropogenic risks identified in Chapters 3 and 4, the population is also faced with genetic risks as a result of its reduced haplotype diversity (Krüger *et al.* 2014b). It is essential to maintain high levels of genetic diversity for the long-term persistence of the population in southern Africa. A significant loss in genetic diversity may decrease fitness or limit the long term capacity of the population to respond to environmental challenges or chance environmental or demographic events in the short term thus affecting survival and reproduction in the long term (Alexandre *et al.* 2007). The low diversity at the mitochondrial level suggests the threats that the population has, and is, being subjected to have had a real impact on the genetics of this population and that management measures must be considered to increase the long-term viability of the population. The dire population trajectory revealed by the population models in Chapter 6 suggests that a programme of supplementation might be a useful strategy to reduce the probability of

extinction in this population, if coupled with improved survival rates and productivity. This programme could include the collection of second eggs or captive breeding with a founder population from elsewhere in the species' range. East and southern African populations share the same haplotypes, therefore the apparently large Ethiopian population could be considered as a source population for captive breeding/introductions to improve diversity. However, other populations globally need not be ruled out because although there may be morphological differences, Chapter 5 has confirmed previous findings that there is not enough genetic variation within the species to warrant the classification into sub-species.

Chapters 2-4 attribute the population decline to anthropogenic activities. However, to gain a more comprehensive understanding of the dynamics, I also attempted to understand the productivity of the population and the survival rates of different age classes. Chapter 6 confirmed that low recruitment and low survival were both likely to be contributing to the low population growth rate. Specifically, Chapter 6 confirmed that nesting success rates had apparently declined over the last 30 years with only 0.55 y/pr/yr now being produced compared to the previously recorded productivity which was 0.89 y/pr/yr. Although it should be noted that these changes may be biased due to the limited extent and location of the study area (in the core of the range) in the past. Despite this apparent reduction, however, our productivity is still within the range recorded for other Bearded Vulture populations (0.43–0.65 y/pr/yr) (Brown 1977, Brown *et al.* 1982, Heredia 1991, Terasse 1991, Margalida *et al.* 2003) although it is at the lower end of the scale (0.55 y/pr/yr). The main reason for these lower levels is because, unlike in the past and unlike many other populations, pairs currently seem to attempt to breed only every second year. Since nesting success is comparatively high (76%), measures that encourage the birds to breed annually should be urgently considered (see below). In addition, training is required to enable observers to better interpret their observations at nest sites to reduce observer bias and increase confidence in these results, enabling a larger sample size to be used for similar analyses in future.

Data on demographic parameters collected during 2000-2014 provided the necessary information to calculate age-specific survival rates to more accurately model growth rates for the population. Half ($n=10$) the birds tagged during the study period died, which provided a means to calculate survival estimates which, even though the sample size was small, provided some indication of survival. The population growth rate projected in Chapter 6 for the next 50 years was negative ($\lambda=0.99$) with a high probability of extinction (0.89) during this period. These extremely dire results point to the need for urgent intervention to ensure a positive population growth rate. All possible resources need to be mobilized to 1) improve the survival of all age classes 2) improve the proportion of breeding birds, and 3) establish a captive breeding programme to supplement the population. A number of recommendations are detailed below for implementation across the species' range aimed at achieving the three points above, all of which need to be implemented simultaneously in a multi-pronged strategy to effect a positive population growth. The strategy must include education and law enforcement aimed at reducing poisoning incidents and testing whether supplementary feeding will reduce risk exposure and increase productivity.

Recommendations for Future Management

Many of the recommendations that I feel are critical to the conservation of the southern African Bearded Vulture population were made in Chapters 2-5. In Chapter 6, I explore which of these recommendations might have the best chance of achieving the desired impact of stabilising the population growth rate in the short term. Of the hypothetical population trajectories that I compared over the next 50 years, a 40% reduction in mortality together with a 15% increase in productivity and the supplementation of four individuals was predicted to result in a positive growth rate ($\lambda=1.07$) with a low (0.43) probability of extinction. The results from Chapters 3, 4 and 6 discussed above suggest that unnatural mortality factors are limiting the population. Therefore the threats of poisoning and power

line collisions need to be mitigated sufficiently to reduce mortality rates by 40% across all age classes. Measures aimed at improving productivity by 15% include reducing human activities, such as helicopter flights and mountaineering, close to nest sites at the beginning of the breeding season and placing supplementary food close to nest sites early in the breeding season. Supplementary food provision near nest sites will ensure that 'safe' food is provided to adults during the breeding season reducing the need to forage wider and be exposed to threats of poisoning. Although food shortage was not found to be a major factor driving the abandonment of territories in Chapter 3, developing additional supplementary feeding sites may benefit the population by improving productivity and reducing the risk of exposure to human persecution and poisoning incidents, particularly for immatures and sub-adults, the high risk age classes. Whether this action would achieve the stated aims, would need to be monitored as part of an adaptive management framework. This action should also be implemented with caution based on the negative impacts of supplementary feeding sites on breeding adults shown by Oro *et al.* 2008.

Paramount to the survival of this population, however, is a reduction of poisoning incidents. Recommendations to address the threat of poisoning have been discussed at a number of meetings/workshops recently (e.g. International workshop on poisoning and vultures in Spain, April 2014; Workshop on poisoning at the Birds of Prey programme annual symposium in Namibia, May 2014) and are as follows: Regulate the import, manufacture and use of poisons including agricultural chemicals and pharmaceutical products known to be lethal to vultures. Legislate and enforce stringent measures to prosecute and impose harsh penalties on perpetrators of poisoning and those illegally trading in vulture parts. Explore alternative, effective and legal predator control measures. Focus outreach programmes on educating the collectors and users of vulture parts, herders that believe vultures kill stock, and farmers using poisons illegally. These recommendations should be focussed in the priority areas that were identified for adults and non-adults in Chapter 4 and discussed above. In addition the use of lead ammunition, as a source of poisoning, needs to be addressed by informing the hunting fraternity, farmers and protected area managers

involved in culling of the threat of lead and focussing on efforts to make alternative lead-free ammunition readily available in the short term. However, it is essential that lobbying takes place at a national level aimed at banning lead ammunition, as has been done in North America and many European countries.

To address the threat of continuous development and encroachment into the core range of the species, proposals for infrastructural development (e.g. houses, power lines, wind farms) and activities (e.g. helicopter flights, cable-way developments) must either be; i) rejected if the impacts cannot be adequately mitigated, ii) sited in the most appropriate location to avoid or minimize negative impacts (e.g. Reid *et al. in review*), and iii) constructed with acceptable (raptor friendly) mitigation measures. Existing unsafe infrastructure must be identified proactively and modified/mitigated accordingly. A valuable partnership already exists with Eskom and the Endangered Wildlife Trust (van Rooyen and Smallie 2006) which must be strengthened and expanded to include the Lesotho Electricity Corporation. Priority areas to be targeted for mitigation can be identified using the habitat use model developed by Reid *et al. (in review)* which predicts important areas of Bearded Vulture use that may conflict with wind turbines. This model can be adapted for other energy infrastructure.

Augmentation of the southern African population is a management option which could be an effective strategy (see Hirzel *et al.* 2004, Schaub *et al.* 2009) and deserves consideration. Since there is little genetic differentiation between populations globally, a broad source population could be considered for this purpose. Augmentation to increase the population growth rate and maintain sufficient genetic variability should be considered as a future management objective and requires further investigation. Based on the high probability of extinction in the short term in the event of no management intervention, the implementation of a captive breeding programme and/or the removal and rearing of the second egg should also be considered a priority in an effort to conserve a representative sample of the population.

Increasing public awareness at all levels of society (from schools to politicians) around the threats to vultures will enlist their support in addressing these threats and obtaining the necessary economic resources to protect the species. An example of this is International Vulture Awareness Day which is held annually across the globe.

The BMP for the species must be used as a tool to ensure the collaboration between Lesotho and the three provinces of South Africa to achieve the goals and objectives of the plan. It is essential that the BMP follows a similar legal approval and adoption process in Lesotho to ensure commitment to implement the plan at government level. The combined efforts of both countries in the implementation of the BMP should be maintained through the Bearded Vulture Task Force.

Flagship Species as a Conservation Strategy

Conservation actions are dependent on economic, political, and social support to provide the necessary funding required to achieve species' conservation targets (Fleishman *et al.* 2011). Economically, species that provide tangible benefits receive priority, *i.e.* "if it pays it stays". Legally, conservation relies on policies that address species conservation. Politically and socially, conservation relies on societal values, aesthetic and commercial standards that determine which species deserve conservation (Small 2011). Therefore as much as humans are the primary cause of species' extinctions, it is societal values regarding natural resources that can be used to influence the extinction process. Once public support has been obtained, political and economic support should follow.

The 'flagship species' approach is a worthwhile approach to gain public support to conserve a species and its habitat. This approach involves using charismatic species to win public favour for specific conservation efforts (Mittermeier 1986). The flagship species approach is similar to the 'umbrella species' where the focus is on typically large animals, requiring a lot of habitat and generally sharing a lot of living requirements with other organisms in their range so that by protecting a larger area, other species are protected as well (Shrader-Frechette and McCoy 1993). Umbrella species are often easily observed or

sampled, they have large home ranges, a long lifespan and their biology is well known. These species are not necessarily the ones facing the biggest threat, however, in the case of the Bearded Vulture conservation efforts focussed on this charismatic (Figure 7.2) and Critically Endangered species will raise the profile of the species and its plight as well as benefitting mountain habitats and the other scavengers and raptors within them. For example the globally endangered Cape Vulture *Gyps coprotheres* is a colonial cliff nesting vulture which also occurs in the Maloti-Drakensberg mountains. This species is exposed to similar threats to those identified in this thesis for Bearded Vulture (e.g. Mundy *et al.* 1992, Boshoff *et al.* 2011), therefore any conservation actions aimed at the Bearded Vulture will also benefit the Cape Vulture.



Figure 7.2 The charismatic Bearded Vulture *Gypaetus barbatus*.

Simberloff (1998) suggested using keystone species as a slightly different approach to gain support for single-species management. In many ecosystems, certain species have impacts on many others, therefore such an approach may unite the best features of single species and ecosystem management. The Bearded Vulture may not necessarily fit the criteria of a

keystone species, species whose presence and role within an ecosystem has a disproportionate effect on other organisms within the system, but they could be used as a flagship or umbrella species in a similar way. The Bearded Vulture being undoubtedly the most charismatic of all vulture species could be used to epitomise vultures generally in efforts to address the “African Vulture Crisis”.

Recommendations for further study

A summary of the recommendations for future research is as follows:

- Since laying rate was calculated based on a small sub-sample of sites, a larger sample size of reliable data from trained observers is required to monitor the effect of management actions on productivity.
- Further research should be undertaken on determining whether the factors affecting survival are also affecting productivity, *i.e.* is productivity low as a result of adult mortality rather than disturbance at the nest site or lack of food.
- Although food shortage was found not to be associated with territorial abandonment, its role in influencing productivity or recruitment through non-adult survival deserves further investigation.
- There was also no evidence to suggest that global warming is driving the abandonment of territories, but the influence on other aspects of the species' demography such as productivity or survival is warranted.
- Continued tracking of the population will provide better survival estimates over time which is essential for modelling population growth. In Chapter 6, age-specific survival estimates were heavily influenced by the death of one or two individuals. Continued tracking will also provide further information on mortality causes as well as data on avoidance rates of new infrastructure such as wind farms, several of which are proposed (and one approved) for development in the species' range.
- A research project dedicated to exploring lead levels in Bearded and Cape Vulture is required to identify the sources of lead contamination in the environment, as many

birds in this study showed high levels of lead exposure. The research should focus on spatial and temporal differences in lead exposure as well as examining other aspects apart from lead levels in blood and bone, such as lead deposits in egg shells.

- Nuclear markers should be explored to further inform questions on the genetics of the southern African population; such as whether the population is inbred and whether nuclear diversity is as low as mitochondrial diversity was found to be.
- Continued monitoring of the status and demography of the population is essential to evaluate the success of the implementation of the management actions that have been recommended above. Monitoring results should be used in the 5-year review cycle of the BMP-S to inform future actions as part of an adaptive management approach.

Conclusions

This work has demonstrated the importance of focussing on small populations, declining populations and populations at the periphery of a species' range. The African haplotypes are possibly the major links within the global Bearded Vulture genetic network and the diversity pattern hints at Africa being the ancestral population which provides support for managing this peripheral population. My investigation into the decline of the Bearded Vulture in southern Africa has demonstrated the value of single-species research and the use of a number of different approaches to identify the mechanisms of decline and predict population trends. Recommendations to address the species demise have been made, including the use of the umbrella/flagship species approach to gain support for its conservation amongst a host of other priority species or economic and development challenges.

This study has provided the necessary information to enable conservationists to focus their interventions on specific issues and locations that will have the highest impact. In so doing this study has also provided the evidence-base to justify the management

recommendations. As such this study contributes to achieving the objectives of the IUCN's Vulture Specialist Group and the Endangered Wildlife Trust's Biodiversity Management Plan for the Species (Krüger 2013) which will add value to Bearded Vulture conservation strategies locally and internationally, and vulture conservation strategies in Africa. My research is timely in an era where the decline in vulture populations is increasingly being recognised as one of the most pressing issues in avian conservation globally and in Africa in particular.

References

- Alexandre R, Couvet, D and Sarrazin F (2007) Integration of demography and genetics in population restorations. *Ecosci* 14: 463–471.
- Allan DG and Jenkins AR (2005) Preliminary report on a survey of breeding sites of Bearded and Cape Vultures in Lesotho. Durban Natural Science Museum, Durban, *unpubl report*.
- Anderson MD (2000) Bearded Vulture *Gypaetus barbatus*. In: Barnes KN (editor) The Eskom Red Data book of birds of South Africa, Lesotho and Swaziland. Birdlife South Africa, Johannesburg, pp. 39-41.
- Bell BD and Merton DV (2002) Critically endangered bird populations and their management. In: Norris K, Pain DJ (editors) Conserving Bird Biodiversity. General principles and their application. Cambridge University Press, Cambridge UK.
- Boshoff AF, Minnie JC, Tambling CJ and Michael M (2011) The impact of power line-related mortality on the Cape Vulture *Gyps coprotheres* in a part of its range, with an emphasis on electrocution. *Bird Conserv Int* 21: 311–327.
- BirdLife International (2014) IUCN Red List for birds. Downloaded from <http://www.birdlife.org> on 05/08/2014.

- Brown LH (1977) The status, population structure, and breeding dates of the African lammergeier *Gypaetus barbatus meridionalis*. *Raptor Res* 11: 49-58.
- Brown CJ (1991) An investigation into the decline of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Biol Conserv* 57: 315-337.
- Brown CJ (1997) Population dynamics of the Bearded Vulture *Gypaetus barbatus* in southern Africa. *Afr J Ecol* 35(1): 53-63.
- Brown LH, Urban EK and Newman K (1982) The birds of Africa, Vol. 1. Academic Press, New York.
- Carrete M, Grande JM, Tella JL, Sánchez-Zapata JA, Donazar JA, Díaz-Delgado R and Romo A (2007) Habitat, human pressure, and social behavior: partialling out factors affecting large-scale territory extinction in an endangered vulture. *Biol Conserv* 136(1): 143-154.
- Fleishman E *et al.* (2011) Top 40 Priorities for Science to Inform US Conservation and Management Policy. *Biosci* 61(4): 290-300.
- Heredia R (1991) Chapter 2 Biología de la Reproducción. In: Heredia R and Heredia B (editors) El Quebrantahuesos (*Gypaetus barbatus*) en los Pirineos. ICONA, Madrid.
- Green RE, Newton I, Schultz S, Cunningham AA, Gilbert M, Pain DJ, Prakash V (2004) Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. *J Appl Ecol* 41: 793–800.
- Hirzel AH, Posse B, Oggier P-A, Crettenand Y, Glenz C and Arlettaz R (2004) Ecological requirements of reintroduced species and the implications for release policy: the case of the bearded vulture. *J Appl Ecol* 41: 1103-1116.
- Krüger S (2006) The 2005 Bearded Vulture (*Gypaetus barbatus meridionalis*) Ground Survey, South Africa. Ezemvelo KZN Wildlife, *unpubl report*.

- Krüger S (editor) (2013) Biodiversity Management Plan for the Bearded Vulture (*Gypaetus barbatus meridionalis*) for Southern Africa. Published 8 May 2014 Government Gazette Notice No 37620.
- Krüger S (*in press*) Bearded Vulture. In Taylor MR (editor) The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. BirdLife South Africa, Johannesburg.
- Krüger S, Piper S, Rushworth I, Botha A, Daly B, Allan D, Jenkins A, Burden D, Friedmann Y (editors) (2006) Bearded Vulture (*Gypaetus barbatus meridionalis*) Population and Habitat Viability Assessment Workshop Report. Conservation Breeding Specialist Group (SSC/IUCN)/CBSG Southern Africa, Endangered Wildlife Trust, Johannesburg.
- Krüger SC, Allan DG, Jenkins AR and Amar A (2014a) Trends in territory occupancy, distribution and density of the Bearded Vulture *Gypaetus barbatus meridionalis* in southern Africa. *Bird Conserv Int* 24: 162-177. doi:10.1017/S0959270913000440.
- Krüger SC, Wesche PL and Jansen van Vuuren B (2014b) Reduced genetic diversity in Bearded Vultures *Gypaetus barbatus* in Southern Africa. doi: 10.1111/ibi.12200.
- Margalida A, García D, Bertran J and Heredia R (2003) Breeding Biology and success of the Bearded Vulture *Gypaetus barbatus* in eastern Pyrenees. *Ibis* 145: 244-252.
- Mittermeier RA (1986) Primate conservation priorities in the Neotropical region. In: Benirschke K (editor) *Primates: the Road to Self-sustaining Populations*, Springer-Verlag, New York, pp. 221-240.
- Mundy P, Butchart D, Ledger J and Piper S (1992) *The Vultures of Africa*. Russel Friedman Books CC, Johannesburg, South Africa.
- Newton I (1979) *Population ecology of raptors*. T and AD Poyser, Berkhamsted.

- Schaub M, Zink R, Beissmann H, Sarrazin F and Arlettaz R (2009) When to end releases in reintroduction programmes: demographic rates and population viability analysis of bearded vultures in the Alps. *J Appl Ecol* 46: 92-100.
- Shrader-Frechette KS and McCoy ED (1993) *Method in Ecology. Strategies for Conservation*. Cambridge University Press, Cambridge.
- Simberloff D (1998) Flagships, umbrella and keystones: is single-species management passé in the landscape era? *Biol Conserv* 83(3): 247-257.
- Small E (2011) The new Noah's Ark: beautiful and useful species only. Part 1. Biodiversity conservation issues and priorities. *Biodiversity* 12(4): 232-247.
- Taylor MR (editor) (*in press*) *The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland*. BirdLife South Africa, Johannesburg.
- Terrasse JF (1991) Chapter 11. Le Gypaete Barbu dans les Pyrenees Francaises. In: Heredia R and Heredia B (editors) *El Quebrantahuesos (Gypaetus barbatus) en los Pirineos*. ICONA, Madrid.
- van Rooyen CS and Smallie J (2006) The Eskom – Endangered Wildlife Trust Strategic
Watson 1990, Partnership in South Africa: A brief summary. *Nature and Faune* 21(1): 25.



Photo 8 Juvenile Bearded Vulture taking off from a Drakensberg cliff